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Lasse Frost Eriksen

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Thesis for the degree of
Philosophiae Doctor
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Lasse Frost Eriksen

Skatval, December 2023

Summary

Ongoing climate change can be expected to have major consequences for many species and ecosystems. Effects have been reported on fecundity, mortality and movement ecology, with potential impacts for population dynamics and species interactions. Mountains are among the ecosystems that are expected to be particularly exposed to climate change, and observed changes include increased temperatures, shorter winters, reduced snow cover, and changed precipitation patterns. For many montane species there is limited information of the relationships between climatic variation and life history traits and demography. Such lack of knowledge makes it challenging to predict population dynamics under a changing climate, and potentially mitigate the effects of climate change.

In this thesis, I investigated how short-term variation in climatic factors affects life history traits and demography of willow ptarmigan (*Lagopus l. lagopus*). Willow ptarmigan is a common and iconic bird species in northern hemisphere mountains, with long-term population declines at least in parts of its distribution range. It is resident to Arctic and low-alpine tundra, including the tundra-forest ecotone, but can perform shorter seasonal migrations within these environments. Empirical research on the detailed responses of ptarmigan to climatic variation is so far limited. I used data from two study areas in Norway, one historical (Dovrefjell, 1978-1994) and one ongoing (Lierne, 2015-2021), to test hypotheses related to reproductive strategies, movement strategies and survival in seasonal environments, with particular focus on the role of climatic variation.

I tested hypotheses that contrasted state-dependent vs common optimal clutch sizes, and found support for a common clutch size across individual. The number of eggs laid was independent of body mass or age (i.e., the state variables), and climatic variables. Still, clutch sizes were limited to a level lower than the theoretical optimum predicted by the model. Although females with high body mass did not produce more eggs, they did produce more hatchlings from large clutches than females with low body mass. Further, I found that increased spring temperatures advanced onset of egg-laying, and that early egg-laying was followed by a higher number of offspring. Both timing of egg-laying and clutch size were highly repeatable within individuals, suggesting that individual quality influenced reproductive strategies.

I demonstrated that willow ptarmigan selected for well-covered nest sites and for nest sites among trees. As a relative measure of how strongly the individuals selected, I calculated individual nest site selection scores based on the relative availability of nest cover and habitat features. The nest site selection scores were not clearly affected by individual characteristics (age or body mass) or climatic variation. I did, however, find that nest site selection scores were related to nesting success, where successful nests were characterized by stronger nest site selection, in addition to a positive effect of an early arrival of spring.

The study population in Lierne was partially migratory, and the probability that juveniles migrated increased with lower body mass. Migratory strategy for adults was not affected by body mass. There was high repeatability in migratory strategy between seasons. Migrants and residents did not differ in terms of clutch size or nesting success.

When the snow arrived early in the previous autumn, there was a delayed mortality risk during spring for yearlings, but not adults. This is hypothesized to be caused by a reduced access to nutrient-rich food after the arrival of winter, with negative effects on resource accumulation and body condition, resulting in a carry-over effect on spring mortality risk. For both yearlings and adults, spring mortality risk also increased with increased snow depth during spring, which may reflect limited access to food resources in a time when body mass reserves are low after the winter. I found no relationship between snow depth and autumn mortality risk.

The findings presented in this thesis suggest that the study species is sensitive to short-term variation in climatic factors, in terms of both seasonal survival and annual reproduction. In light of the projected climatic changes in the future, the results *per se* may apparently point in a positive direction for willow ptarmigan, where earlier and warmer springs increase reproductive success, and a later arrival of snow in the autumn and less snow in the spring increase survival prospects. However, such interpretations should be made with caution, because responses in vital rates to climatic factors may involve a complex set of ecological mechanisms and trade-offs between life history traits; the same climatic factor may give different age-specific effects on vital rates over a lifespan, and give contrasting effects on different vital rates. The same climatic factor could also influence vital rates of the focal population indirectly, through effects on competing species or other trophic levels in the food web (e.g., predators, food plants and insect prey). My results underline the need for integrated approaches where the effects of climatic factors are investigated on multiple demographic rates simultaneously, in different life stages of the focal species, and to take into account interspecific interactions. This may provide further information on how climatic factors affect trade-offs between life history traits, and may improve our understanding of the vulnerability of willow ptarmigan and the mountain ecosystems to climatic changes.

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Appendices: Papers I - IV

List of papers

I. **Eriksen, L. F.**, T. H. Ringsby, P. F. Moa, and E. B. Nilsen. Nest site selection and nesting success under climatic variation in willow ptarmigan Lagopus l. lagopus. *Submitted.*

II. **Eriksen, L. F.**, T. H. Ringsby, H. C. Pedersen, and E. B. Nilsen. 2023. Climatic forcing and individual heterogeneity in a resident mountain bird: legacy data reveal effects on reproductive strategies. Royal Society Open Science 10:221427.

III. Arnekleiv, Ø., K. Eldegard, P. F. Moa, **L. F. Eriksen**, and E. B. Nilsen. 2022. Drivers and consequences of partial migration in an alpine bird species. Ecology and Evolution 12:e8690.

IV. **Eriksen, L. F.**, T. H. Ringsby, M. F. Israelsen, P. F. Moa, V. Grøtan, and E. B. Nilsen. Climatic variation affects seasonal survival of an alpine bird. *Manuscript.*

Declaration of contributions

I. EBN conceived the main idea, and all authors took part in the conceptualization of the study. LFE, PFM and EBN led the data collection, and LFE and EBN curated the data. LFE led the formal analysis, with support from EBN. LFE created the visualizations. LFE wrote the manuscript, with support and supervision from all co-authors. All authors approved the final version of the submitted manuscript.

II. EBN conceived the main idea, and LFE, EBN and THR developed the concept. HCP led the historical field project and LFE digitized the raw data. LFE analyzed the data, with supervision from EBN and THR. LFE created the visualizations. LFE wrote the original draft, with comments and contributions from all co-authors. All authors approved the final version.

III. All authors took part in conceptualizing the study. LFE, PFM and EBN led the field data collection, and LFE and EBN curated the data. EBN and PFM administrated the project. ØA analyzed the data with support and supervision from EBN, KE and LFE. ØA created the visualizations, with support from EBN and KE. ØA wrote the original draft, with revisions led by EBN, and with contributions and supervision from EBN, KE, LFE and PFM. All authors approved the final manuscript.

IV. LFE, EBN, PFM and THR developed the idea. All authors took part in the conceptualization of the study. LFE, MFI, PFM and EBN led the field data collection in different periods, and LFE, MFI and EBN curated the data. EBN and PFM administrated the project. LFE led the formal analysis with contributions from EBN, and support from VG, THR and MFI. LFE created the visualizations. LFE wrote the original draft, and revised the draft based on comments and contributions from all co-authors.

Introduction

Life history traits in seasonal environments

Life history theory aims to explain how evolution shapes organisms to optimize their survival and reproduction, with limited resources available, in order to maximize fitness (Stearns 2000). Important life history traits include, for instance, age and size at maturity, age- and size-specific reproductive investment, survival rates in different ages, and lifespan (Curio 1983, Roff 1992, Stearns 1992, Healy et al. 2019). Trade-offs among life history traits involve fitness costs and benefits and affect resource allocation to growth, self-maintenance and reproduction across time, shaped by natural selection to maximize fitness (van Noordwijk and de Jong 1986, Daan et al. 1990, Lemaître et al. 2015). For instance, high adult mortality rates may impose a selective pressure promoting low age and small size at first reproduction (Reznick et al. 1990). Thus, life history traits are often connected to each other in characteristic combinations deciding the pace of life, for instance a combination of early maturation, high reproductive investment and high mortality (Stearns 1983, Bielby et al. 2007, Réale et al. 2010, Healy et al. 2019). Evolution of life history traits are caused by selective pressure from factors that are extrinsic or intrinsic to the individual (Stearns 2000). The intrinsic factors include evolutionary constraints and trade-offs between traits, while the extrinsic factors include for instance predation, access to resources or climatic effects. For both intrinsic and extrinsic factors, seasonality often plays an important role (Varpe 2017), as environmental variability through the year can lead to variation in for instance availability and acquisition of resources, reproduction (Paper I and II) or survival patterns (Paper IV).

Reproductive success depends on a number of factors, among them investment in the number of offspring (Westneat et al. 2014). Variation in the number of offspring is assumed to be closely related to variation in food availability (Lack 1948), where access to nutrients may shape trade-offs between, for instance, current vs future reproduction (Nur 1984, Creighton et al. 2009, Duffield et al. 2017). Individual state variables such as age or body condition may affect both an individual's ability to acquire resources and how the limited resources are allocated between growth, self-maintenance and reproduction (Curio 1983, van Noordwijk and de Jong 1986). As variation in state among individuals may affect resource acquisition and trade-offs, individual optimization of number of offspring could be expected (van Noordwijk and de Jong 1986, Pettifor et al. 1988). However, some studies suggests that the number of offspring can also be independent of individual state if environmental conditions during the breeding season are unpredictable (Gaillard et al. 2014). These aspects were investigated in Paper II, where I focused on how variation in individual state and weather conditions influenced clutch size and number of chicks produced in a montane bird.

In seasonal environments, reproductive strategies also involve choosing a favorable time and location for breeding. For birds, timing of breeding may affect reproductive success, where early breeding usually leads to more offspring (Klomp 1970, Winkler and Walters 1983, Verhulst and Nilsson 2008). Breeding later in the season may also be traded-off against the potential cost of failure if the main insect peak is missed (e.g., Both et al. 2009, Visser and Gienapp 2019), or if there is not sufficient time for offspring growth during summer (Perrins 1970). There is strong evidence for variation in timing of breeding due to variation in environmental conditions (e.g., Visser et al. 1998, Crick and Sparks 1999). However, timing can also vary among individuals of different age or body mass (Perdeck and Cavé 1992, Wiebe and Martin 1998a, Bêty et al. 2003, Verhulst and Nilsson 2008), and individuals may be affected differently by environmental conditions. These aspects were investigated in Paper II. Also nest site selection (sensu Johnson 1980) is likely to vary due to variation in individual characteristics and environmental conditions (Forstmeier and Weiss 2004). Nest site selection can be assumed to involve trade-offs, where for instance benefits of easy access to forage may be weighed against costs of exposure to predation. The variation in habitat characteristics in the close surroundings of nest sites has been shown to influence reproductive success (Olsen and Olsen 1989, Wiebe and Martin 1998b), and individual variation in nest site selection may thus result in variation in reproductive success. In Paper I, I focused on whether nest site selection was influenced by variation in individual maternal characteristics or by variation in environmental factors. In addition, I addressed whether nest site characteristics, nest site selection or individual characteristics affected reproductive success.

Effects of climatic variation on life history traits and demography

The current dramatic change in the world's climate may affect the life histories of wild species, and the dynamics of populations and ecosystems (McCarty 2001, Iler et al. 2021, IPCC 2022, Jantzen and Visser 2023). Climatic factors directly and indirectly affect the amount and availability of food resources, and consequently affects both acquisition and allocation of resources to growth, self-maintenance or reproduction (Stearns 1992, Both and Visser 2005). For instance, climatic conditions influence the phenology (i.e., the seasonal timing of recurring events) of abundance peaks of many prey invertebrates and plants (Inouye 2022), that are food resources for species at higher trophic levels (Miller-Rushing et al. 2010). Studies have reported effects of climate change on fecundity and mortality in a range of species and taxonomic groups (Paniw et al. 2021, Halupka et al. 2023). Further, variation in weather conditions among years or seasons can affect species' movement ecology on different scales, with potential effects on population dynamics (Dodge et al. 2014, Somveille et al. 2015, Reid et al. 2018). However, to fully understand climate change effects on wildlife populations, we also need information about individual adaptive capacity through phenotypic plasticity (Dawson et al. 2011). Adaptive capacity has been shown, for instance, as changes to the onset of breeding in a population due to changes in onset of spring (Visser et al. 2009). Such changes may potentially affect reproductive success of a focal species (Winkler et al. 2002, Both and Visser 2005, Reed et al. 2013), although this may not be reflected in population dynamics (Reed et al. 2013, Dunn and Møller 2014). For many species and ecosystems, there is a lack of information relating climatic variation to life history traits and demography (Miller-Rushing et al. 2010, Paniw et al. 2021), making it difficult to predict population dynamics and potentially mitigating the effects of climate change.

One should note that 'climate change' refers to the changes in long-term weather patterns, thus, climate change research should be distinguished from research on biological effects of short-term climatic variation (Haunschild et al. 2016). Research focusing on the effects on species or ecosystems due to climatic variation (i.e., short-term variation in the weather) may for instance inform predictions for a changing climate, but attributing effects directly to the long-term climate change should be done with caution when they are based on inference made from short time-series.

The study species and the mountain ecosystem

Mountains are among the ecosystems that are expected to be particularly exposed to climate change (Adler et al. 2022). A number of studies indicate that warming may be amplified with elevation, leading to more rapid temperature changes in mountains than in lowlands (e.g., Pepin et al. 2015, Toledo et al. 2022). Mountain environments are characterized by low temperatures, strong seasonality with short growing seasons, and limited food availability during winter. In many regions, the ground is covered by snow during winter. However, increased temperatures and changed precipitation patterns in mountains are already noticeable (e.g., Pepin et al. 2015, Adler et al. 2022). Among the observed changes, shorter winters and reduced snow cover in spring are highly influential effects in northern hemisphere mountain ecosystems (Callaghan et al. 2011, Rizzi et al. 2018).

Alpine species are adapted to a life in harsh conditions, with traits shaped by the environmental characteristics of high-altitude environments (Martin and Wiebe 2004). They are expected to be highly sensitive to the ongoing changes in climatic conditions, for instance due to narrow climatic tolerance and range contractions (Pacifici et al. 2017, Scridel et al. 2018, Bradter et al. 2022). As the harsh climatic conditions likely induce strong selection pressures, alpine ecosystems are well-suited for studying climate change effects on life history traits. Willow ptarmigan is an iconic bird species in Arctic and low-alpine tundra, including the tundra-forest ecotone (Fuglei et al. 2020). Although the species has seen a long-term population decline at least in parts of Europe (Lehikoinen et al. 2014, Hjeljord and Loe 2022), it was recently delisted from the European red list (BirdLife International 2021). In Norway, the general trend indicates a slight population increase over the last decade (Nilsen and Rød-Eriksen 2020). Willow ptarmigan is a medium-sized tetraonid (400-800 g), that is relatively short-lived, with a generation time of approximately 1.8 years (Sandercock et al. 2005). They have a relatively fast pace of life; most females start breeding as yearlings (Wiebe and Martin 1998a), clutches are large with 8-12 eggs in a ground nest (Parker 1981, Myrberget 1986a), and annual rates of natural mortality are relatively high (0.53-0.55; Smith and Willebrand 1999, Sandercock et al. 2011). Sensitivity analyses indicate that population growth rate (λ) is most sensitive to variation in juvenile survival from post-fledging until the first breeding, although nesting success and offspring survival until independence are also important factors (Steen and Erikstad 1996, Sandercock et al. 2005).

Willow ptarmigan raise one brood per year, but may renest if the first nesting attempt fails (Parker 1981, Myrberget et al. 1985). Both sexes are territorial during the breeding season (Steen et al. 1985). Males can be either monogamous or polygamous (Tarasov 2003), making male reproductive success more difficult to quantify than female success. After mating, the role of males is apparently limited to predator defense (Pedersen and Steen 1985). The chicks are precocial, but depend on their mother until late summer for thermoregulation and predator defense (Aulie 1976, Pedersen and Steen 1985). When winter arrives, grouping into sex-specific flocks is common for both juveniles and adults (Weeden 1964, Sandercock et al. 2005).

Seasonal migration is common in a wide range of species, and is often assumed to be an adaptation to seasonal changes in the environment (Alerstam et al. 2003, Reid et al. 2018).

Some species may be resident to the same landscape (e.g., mountains), but perform short-distance migrations between summer and winter ranges (Fedy et al. 2012). Further, some populations are partially migratory (Chapman et al. 2011), where only parts of the population migrates between summer and winter areas, while others remain resident. Willow ptarmigan is resident to the mountain ecosystem but may perform short-distance migrations between montane summer and winter areas. The propensity to migrate appears to differ among both populations and individuals (Pedersen et al. 2004, Brøseth et al. 2005, Hörnell-Willebrand et al. 2014), where the decisions to migrate or not may be affected by individual heterogeneity, intraspecific interactions or adaptation to environmental conditions (Chapman et al. 2011, Reid et al. 2018). The migration patterns of willow ptarmigan was focused upon in Paper III.

Willow ptarmigan are affected by both human-induced and natural mortality causes. Harvest mortality is often high (Smith and Willebrand 1999, Sandercock et al. 2011, Israelsen et al. 2020), particularly in easily accessible areas (Breisjøberget et al. 2018a, Frye et al. 2023), and overharvest imposes a well-documented risk (Aanes et al. 2002, Sandercock et al. 2011, Eriksen et al. 2018). Other causes of human-induced mortality include, for instance, collisions with fences (Bevanger and Brøseth 2000), increased predation due to land-use (Støen et al. 2010), climate-induced insect outbreaks and defoliation (Jepsen et al. 2013) or climate-related diseases (Ytrehus et al. 2021).

Predation is an important cause of natural mortality for willow ptarmigan eggs, juveniles and adults (Smith and Willebrand 1999, Munkebye et al. 2003). Their population dynamics are in many regions closely connected with the cycles of small rodents such as lemmings or voles (Arvicolinae), where the cycles are largely affected by predator-prey dynamics (Hagen 1952, Steen et al. 1988, Ims and Fuglei 2005, Kvasnes et al. 2014, Bowler et al. 2020). Historically, these close relationships have been characterized by 3-5 year population cycles (Moss and Watson 2001), but in later years the cycles have been reduced, presumably affected by climate change (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013). Common predators on adult willow ptarmigan include the specialist predator gyrfalcon (*Falco rusticolus*), and the generalists red fox (*Vulpes vulpes*) and golden eagle (*Aquila chrysaetos*) (Langvatn 1977, Henden et al. 2017, Nielsen and Cade 2017, Breisjøberget et al. 2018b).

Willow ptarmigan molt into a white plumage during winter (Zimova et al. 2018). Such seasonal color change is also displayed by several other species residing in northern latitudes, such as hares (*Lepus* spp.), arctic fox (*Vulpes lagopus*) and least weasel (*Mustela nivalis*) (Mills et al. 2013). This adaptation to the seasonality reduces detectability in snowy landscapes, but it also leaves the individuals vulnerable to detection by predators if the timing of the molt is not matched with the seasonal arrival or departure of snow cover (Stokkan 1992). Previous studies have reported such camouflage mismatches in several species (Nielsen and Cade 1990, Mills et al. 2013, Zimova et al. 2016, Atmeh et al. 2018). In case such a mismatch is not reduced through phenotypic plasticity or evolution in color change phenology, negative effects on mortality risk should be expected (Mills et al. 2013).

Willow ptarmigan should be a suitable model species for studying effects of climatic variation for mountain birds, given its circumpolar distribution (Fuglei et al. 2020) and its ecological significance in montane ecosystems (Nielsen and Cade 2017). Although ptarmigans have been much studied through decades (Moss et al. 2010), there are relatively few studies that have investigated how climatic factors influence life history traits and demography in ptarmigan species (Henden et al. 2017). Most such studies have focused on the relationships between climatic factors and rates of population change (Wang et al. 2002, Imperio et al. 2013, Bowler et al. 2020, Henden et al. 2020, Melin et al. 2020) or reproductive output (Novoa et al. 2008, Novoa et al. 2016, Wann et al. 2016). However, the strong seasonal variations in alpine environments may give contrasting effects on demographic rates in different seasons, for instance, seasonal variation in mortality risk. Thus, data should have a relatively high spatio-temporal resolution in order to reveal detailed ecological mechanisms, where for instance yearly data intervals may not be sufficient for many questions. Empirical research on the detailed responses of ptarmigan to climatic variation is thus limited, with a few exceptions (e.g., Fletcher et al. 2013).

Objectives

In this thesis, I study the mechanisms shaping life history traits and demography in northern hemisphere mountain environments. Using willow ptarmigan as a model species, I test hypotheses related to reproductive strategies, movement strategies and survival in seasonal environments, with particular focus on the role of climatic variation.

In Paper I, I studied individual variation in nest site selection during the progress of spring. Further, I investigated whether the nest site selection affected nesting success, and whether this was related to the onset of spring. In Paper II, I tested hypotheses related to maternal reproductive investment and timing of reproduction. Here I analyzed whether climatic variation and individual state variables affected the number of offspring and timing of reproduction. In particular, I tested contrasting hypotheses of common vs state- or weather-dependent clutch size, and how weather conditions and individual characteristics affected reproductive investment and timing of egg-laying. In Paper III, I studied female partial migration, and whether individual migration strategies were related to individual characteristics. Further, it was assessed whether the decision to migrate or not was related to reproductive success. Finally, in paper IV, I investigated variation in mortality risk in the spring and autumn seasons. In this paper I tested whether snow depth and winter arrival affected mortality risk, with contrasting effects of snow due to food limitation or a camouflage mismatch between snow cover and the molting between white and brown plumage.

These complimentary research questions highlight different aspects of the overarching objectives. Combined, these papers will improve our understanding of mechanisms behind responses to climatic variation, and thus provide a wider perspective on the vulnerability of willow ptarmigan and mountain ecosystems to climate change.

Methods and results

Study areas

Figure 1: Location of the study areas, Lierne (northeast) and Dovrefjell, in Fennoscandia.

The four papers were based on willow ptarmigan data from two low-alpine and north boreal (Moen 1999) study areas in central Norway (Fig. 1 and 2). In Paper II, I used data from a historical study area in Dovrefjell, on the eastern borders of Dovrefjell-Sunndalsfjella National Park (central location of the study area: 62°17'N, 09°36'E). This area is approximately 900–1200 m.a.s.l., with a yearly temperature mean of 0.1° Celsius (C) over the study period (weather data in this section is based on historical weather station data from The Norwegian Meteorological Institute, www.met.no). Monthly temperature means in the period were -8.2°C in January, -1.8°C in April, 10.3°C in July and 0.4°C in October. Snow usually covers the ground from October-November to April-May. Mean annual precipitation was 460 mm, and there was usually more precipitation falling as summer rain than winter snow. In Paper I, III and IV, I used data from an ongoing study, centered around Lierne municipality (64°20'N, 13°20'E), 300 km northeast of Dovrefjell. Most of the Lierne study area is in the range of 400-800 m.a.s.l., with a yearly temperature mean over the study period of 2.6°C, and means of -7.1°C in January, 0.7°C in April, 13.3°C in July and 2.9°C in October. Similar to Dovrefjell, there are usually snow-covered grounds in Lierne between October-November and April-May, but with higher mean annual precipitation (940 mm during the study period) that is often evenly distributed between rain and snow within a year. Thus, there is usually much more snow during the winter months in Lierne than in Dovrefjell. The landscape in both areas is a mosaic of open heath and scrub vegetation (Ericaceae, willow shrub *Salix* spp., dwarf birch *Betula nana*), bogs and forest patches. Trees in the higher Dovrefjell area are mainly downy birch *Betula pubescens*, and in the lower Lierne area birch *Betula* spp., Norway spruce *Picea abies*, and Scots pine *Pinus sylvestris*.

Figure 2: Photos from the two study areas during springtime in different years (top right: Dovrefjell, others: Lierne).

Collection of willow ptarmigan data

In the historical study in Dovrefjell (1978-1994), reproducing female willow ptarmigan were monitored during the breeding season. Females on nests were detected by manually searching through known territories (Pedersen et al. 1983). When detected, they were captured, weighed to the nearest 5 grams, and age was classified to either ‘yearling’ (also termed ‘juvenile’, i.e., hatched the previous summer) or ‘adult’ (Bergerud et al. 1963). The number of days the eggs had been incubated was determined based on floatation tests on eggs (Westerskov 1950). Monitoring was then performed by manual observations in the field, and conducted until hatching was completed.

In the ongoing study in Lierne and surroundings (2015-2021), we captured willow ptarmigan in February and March each year and equipped each bird with a VHF transmitter (Fig. 3a). Upon capture, we also measured body mass and classified the age as described above, and determined sex by observing sex characteristics and confirming through the analysis of DNA samples. Marked birds were monitored by use of VHF triangulation and signal type (i.e., alive or mortality signal). Fieldwork was performed at least monthly, except in December and January when few positions were obtained due to short day length and challenging weather conditions. During May and June each year, we conducted several monitoring sessions per month. The number of days the eggs had been incubated was determined as above. Nesting was monitored by use of automated cameras on the nests of radiomarked females (Fig. 3b,c,d), and by inspecting the nests and eggshells after completed hatching. We also monitored nests of unmarked females using the same methods when they were discovered by chance.

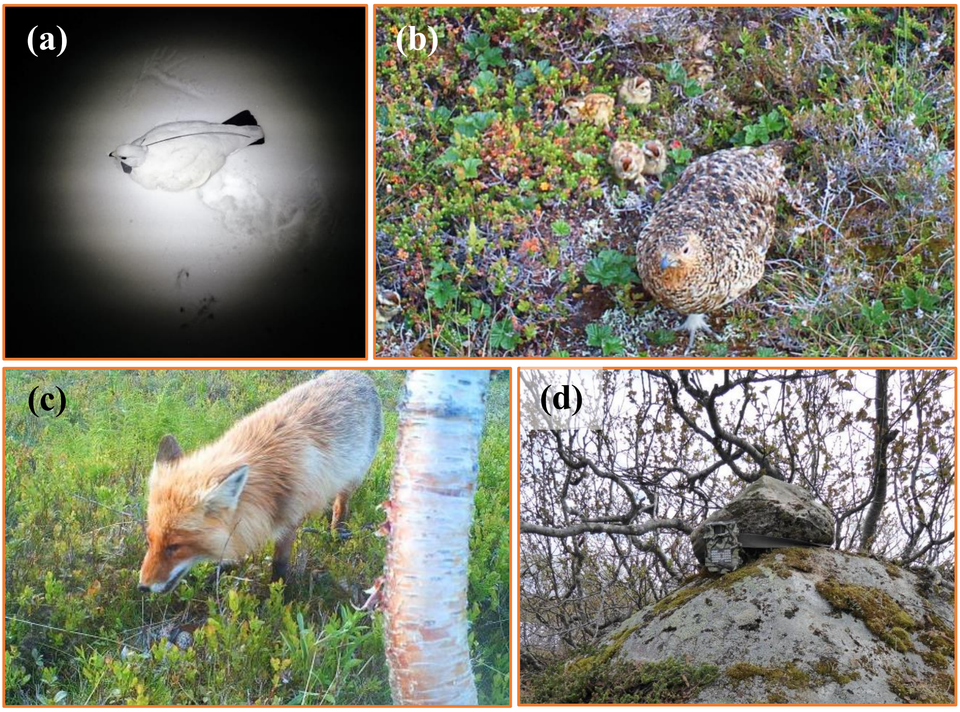

Figure 3: (a) VHF-marked willow ptarmigan. Monitoring by use of automated camera reveals (b) successful nesting with female and hatched chicks, and (c) unsuccessful nesting where the eggs are predated by a red fox. (d) Automated camera monitoring a nest.

See Papers I-IV (and references therein) for a full description of all data collection protocols relevant for each paper.

Paper I

To study nest site selection and nesting success under climatic variation, I used seven years (2015-2021) of individual-based willow ptarmigan nesting data (n=110) from Lierne. To test whether willow ptarmigan selected certain habitat features over others when choosing nest sites, I developed territory-scale nest site selection functions. Here, I compared vegetation and amount of nest cover in used nest sites vs four available locations around each nest. In addition, I developed landscape-scale nest site selection functions, comparing vegetation type from habitat maps in used nest sites and random points within the largest geographical cluster of nests in the study. To test whether nest site selection varied depending on individual characteristics (age or body mass) or environmental variables (NDVI, snow depth, elevation, and year), I first calculated individual nest site selection scores for territory-scale selection of vegetation and nest cover. Then, I used linear models to investigate how these scores varied in relation to the individual characteristics and environmental variables. Finally, I used logistic regression models to assess how nesting success (defining 'success' as at least one chick leaving the nest) varied in relation to the nest site selection scores, vegetation and nest cover, characteristics of the individual female, and environmental variables.

I found that nest site selection occurred at both the territory- and the landscape-scale. At the territory-scale there was a selection for well-covered nest sites, and a selection for nest sites among trees. At the landscape-scale, nest sites in tree habitat were selected for, with nest altitudes following a quadratic curve. The nest site selection scores varied between years (Fig. 4a) but did not seem to be influenced by any of the other variables. My results did, however, indicate that the nest site selection scores were related to nesting success, as successful nests were characterized by stronger nest site selection (Fig. 4b). There was also an effect of climatic variation, where nesting success increased when the spring arrived earlier.

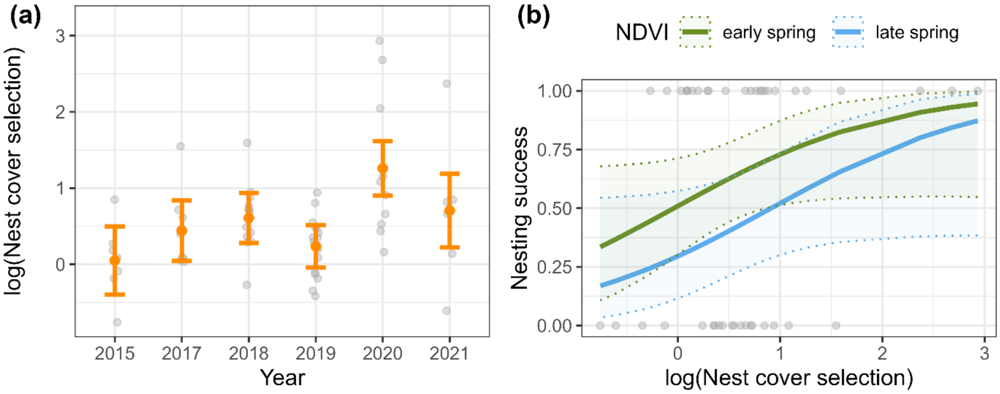

Figure 4: (a) Individual selection scores for nest cover in relation to variation between years, and (b) predicted nesting success in relation to individual selection scores and spring progress, for female willow ptarmigan. The upper and lower quartiles of NDVI values are presented as 'early spring' and 'late spring', respectively. Whiskers (a) and ribbons (b) show 95% confidence intervals (CI) and points show raw data.

Paper II

In paper II, I used the historical 17 year long data set (n=290 breeding females with n=319 breeding attempts) from Dovrefjell to test hypotheses related to maternal investment and timing of reproduction, using willow ptarmigan as a model species. First, I tested two competing hypotheses of clutch size optimization, *common optimal clutch size* vs *state-dependent clutch size* (Gaillard et al. 2014), to assess whether number of eggs laid and number of chicks hatched were common across individuals or dependent on measured individual states (i.e., body mass and age). In addition, I expanded the model by testing whether the number of eggs laid and the number of chicks hatched depended on climatic variables (i.e., mean temperatures and the NAO index). Second, I tested hypotheses regarding variation in timing of egg-laying in relation to body mass, age, and climatic variables (i.e., onset of spring, mean temperatures, and the NAO index). Then, I tested if the number of offspring was related to the chosen timing strategy. In addition, I modelled the relationship between spring temperatures and individual body mass. Third, for testing the hypothesis that variation in reproductive success may be influenced by individual quality (i.e., unmeasured individual characteristics), I estimated repeatability in individual timing of egg-laying and number of eggs laid across breeding attempts.

For my first hypothesis, the results suggested a common clutch size across individuals, where the number of eggs laid was independent of body mass, age, and climatic variables. However, the analysis of the number of chicks hatched indicated that clutch sizes were limited to a level lower than the theoretical optimum predicted by the model. In addition, the results suggested an interaction effect where females with high body mass produced more hatchlings from large clutches than females with low body mass. For my second hypothesis, there was strong support for a weather-dependent timing of reproduction. Increased spring temperatures advanced onset of egg-laying (Fig. 5a), and early egg-laying was followed by a higher number of eggs (Fig. 5b). The results also revealed an unexpected tendency of yearlings to breed earlier than adults. Individual body mass was positively affected by spring temperatures. For the third hypothesis, I found that both timing of egg-laying and number of eggs laid were highly repeatable within individuals, suggesting that trade-offs in reproductive strategies were influenced by individual quality.

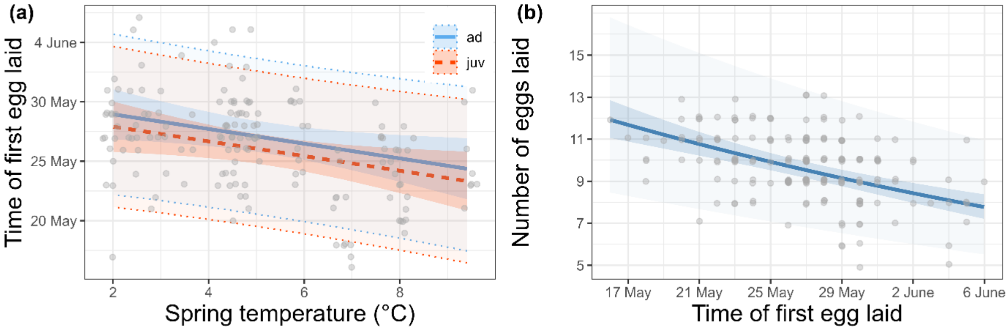

Figure 5: The effects of (a) age group and mean spring temperature (over 15 days) on timing of egg-laying, and (b) timing of egg-laying on clutch size, in willow ptarmigan. Densely colored ribbons show 95% CI for the population level effects of fixed terms, at the mean values of year as random term. Broader lighter ribbons are prediction intervals including random year effects, and points show raw data.

Paper III

To test hypotheses regarding partial migration strategies, we used five years (2015-2019) of data from VHF-marked female willow ptarmigan (n=73), in addition to position data from three GPS-marked birds in winter 2018. We classified January–March as the winter season and May–July as the summer season. Then, we calculated a common winter home range across individuals based on the three GPS-marked willow ptarmigan, and a common summer home range based on VHF-marked birds with ≥3 positions during the summer season. The classification of migratory strategy was based on overlap between the seasonal home ranges, where birds with overlapping home ranges were classified as residents, and otherwise as migrants. We used linear models to test if the decision to migrate or not was related to body mass or age. Further, to test if individuals repeated migratory strategy between seasons, we estimated repeatability with log(movement distance) as response variable, due to non-convergence when using the binary response of migratory strategy. Finally, to test whether reproductive success was affected by migratory strategy, we modelled nesting success in two complimentary model sets, first with number of eggs as response variable, then with success (i.e., at least one hatched chick) vs failure as response variable.

Migratory strategy was related to individual characteristics, where the probability that juveniles migrated increased with lower body mass (Fig. 6). For adults, migratory strategy was not affected by body mass. Further, there was high repeatability of migratory strategy between seasons, also after accounting for potential age effects. There was no difference between migrants and residents in terms of clutch size or nesting success.

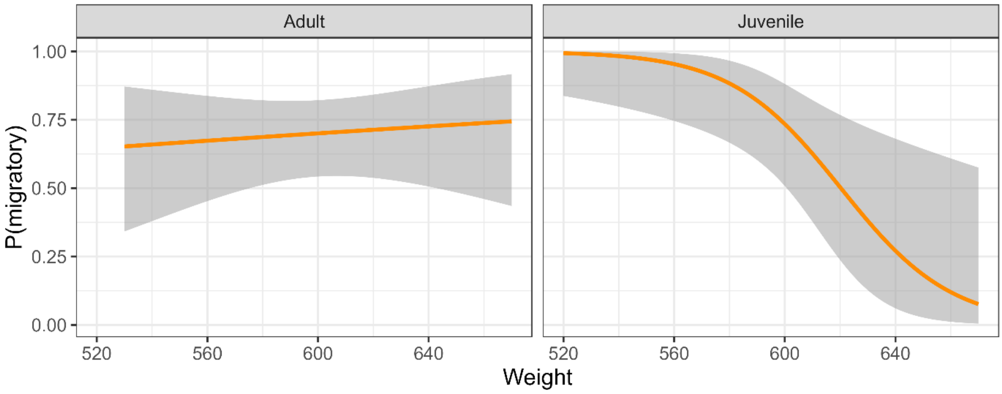

Figure 6: The relationship between body weight (g), age and the probability of migrating (with 95% CI), in female willow ptarmigan. Only transitions from winter to summer are included.

Paper IV

I tested competing hypotheses regarding the effects of climatic variation on mortality risks during spring (15 March – 15 June) and autumn (1 Sept – 15 Dec). I predicted that seasonal mortality risk could either increase with snow depth due to a limited access to nutrient-rich food resources, or decrease with snow depth due to an avoided camouflage mismatch between snow cover and molting between white and brown feathers. Further, I predicted that spring mortality would increase with an earlier arrival of winter in the previous year, as this can be expected to negatively affect spring body condition. To test the hypotheses, I used data from VHF-marked male and female willow ptarmigan (n=272) from Lierne (2015-2021), collected at least monthly except from in the darkest period of winter (December and January). I used data on snow depth with a 1x1 km resolution from the *seNorge* snow model (Skaugen et al. 2018) to estimate the arrival time of winter each year, and to obtain individual-based weekly mean snow depths. Further, I used the NAO winter index (Hurrell 1995) as an additional measure of winter conditions. To account for variation in individual characteristics, I added sex and age group (yearlings *vs* adults) as covariates. I assessed variation in mortality risk within seasons because of climatic variation, with Cox Proportional Hazards models.

I found that the mortality risk for yearling birds in the spring increased when winter arrived earlier in the previous year (Fig. 7a). Spring mortality risk for yearlings increased 38% with a ten day advance in winter arrival. There was no change in adult mortality risk during spring due to the arrival time of winter. For both yearlings and adults, spring mortality risk was positively related to the snow depth (Fig. 7b). Yearlings were generally at higher risk of dying than adults during spring. I did not find an effect of variation in snow depth on autumn mortality risk, but my results show that males were at almost three times higher risk than females during autumn.

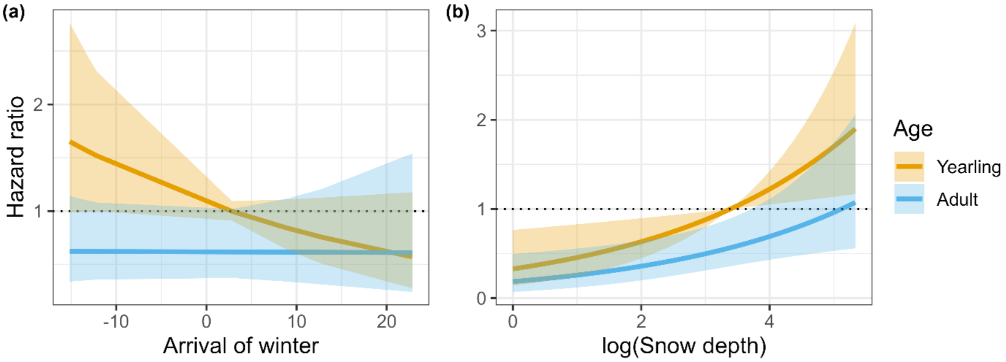

Figure 7: Mortality risk for willow ptarmigan during spring (15 March – 15 June) for the years 2015-2021 in Lierne. Hazard ratios with 95% CI for the two highest ranking models from the model selection procedure are shown. Dotted horizontal lines show the baseline hazard. Arrival of winter (a) is shown as the number of days deviation from the mean arrival of snow in autumn over the study years. In (b), the x-axis shows log-transformed snow depth in cm.

Discussion

There is an urgent need for knowledge about the effects of a changing climate on species and ecosystems. Research on effects of short-term variation in climatic factors is useful to indicate relationships and inform future predictions. In this thesis, I have examined whether short-term variation in climatic factors affects life history traits and demography of willow ptarmigan. Individual-based data with high spatial and temporal resolution have allowed me to put forward and test hypotheses regarding reproduction, survival and migration strategies.

Reproductive success

The willow ptarmigan females in the Lierne study area selected mainly for well-covered nest sites, and for nest sites in the close vicinity of trees (Paper I). The selection of nests with better cover seems to be a general feature for many grouse species (Paper I, Schieck and Hannon 1993, Anich et al. 2013, Dinkins et al. 2016), and can be assumed to be caused by the predation risk (Wiebe and Martin 1998b). The choice of nesting among trees in our Lierne study population, is not consistent with the findings of a previous willow ptarmigan study (Steen et al. 1985), although different vegetation composition and categorization between the studies make direct comparisons difficult.

By estimating nest site selection scores, I found that a higher score for nest cover was associated with higher nesting success (Paper I). This indicates that nest site selection is under natural selection in the study population. The selection for nest cover was particularly high in 2020 (cf. Fig. 4a), which was by far the year with the latest arrival of spring during the study period, but in general spring phenology did not clearly affect nest site selection. Spring phenology did, however, affect nesting success, with lower nesting success in late springs. The lack of a clear relationship between spring phenology and nest site selection strength may indicate that there is limited capacity to adapt the nest site selection strategy to the variation in onset of spring. As such, we cannot expect that nest site selection will compensate for decreased nesting success due to a late arrival of spring.

Nesting experience may affect the selection of nest sites in environmental space for willow ptarmigan. There were few repeated nesters in the data, but there were indications that increased nesting experience might be related to a narrower preference of nest site habitat, with a higher frequency of nest sites among trees for more experienced females (Box 1). In geographic space, nest site fidelity is high in willow ptarmigan (Box 1, Schieck and Hannon 1989). This could indicate limited plasticity in nest site selection, which may potentially be problematic under climate change. If climatic factors do not directly influence the choice of nest site, then chosen nest sites may not represent the most suitable nest sites in a given year. For instance, in a year with a late arrival of spring it might be favorable to nest at a lower altitude to be able to initiate breeding earlier, which may not occur if there is limited plasticity in nest site fidelity.

Box 1: Repeatability in nest site selection in Lierne

I examined repeatability in spatial distribution between nesting occasions for female willow ptarmigan with more than one recorded nesting. 56% of the individuals showed a relatively strong breeding site fidelity, where they chose nest sites in close geographical proximity (measured as euclidian distance) to previous nests (n=18 individuals, range 11-1724 m, median distance 109 m, mean distance 406 m). There were no indications that spring progress, other year-effects or previous nesting success affected the distance between nest sites. The individuals did not display the same repeatability in use of environmental space. Here, the main tendency was that the former nest habitat mirrored the distribution of the total sample of individuals in the study, but they more often chose nest sites among trees in the latter nesting occasion (n=17, Fig. B1).

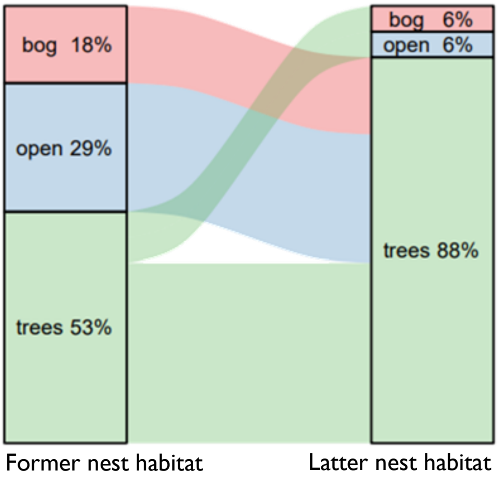

Figure B1: Change in nest site habitat between nesting occasions for individual female willow ptarmigan in Lierne.

To maximize fitness, timing of egg-laying and determining clutch size are the two major decisions made by individual birds during reproduction (Daan et al. 1990). I found that higher spring temperatures were associated with earlier timing of egg-laying (Paper II), in line with a number of previous studies (e.g., Crick and Sparks 1999, Visser et al. 2009, Fletcher et al. 2013). Further, both clutch sizes and the number of hatched chicks increased with early egg-laying (Paper II, Klomp 1970, Winkler and Walters 1983). The two study areas, Dovrefjell and Lierne, are located 300 km apart and at different altitudes. Still, the two study areas show high similarity in timing responses to spring temperatures and clutch size responses to timing (Box 2). Along with previous studies pointing in the same direction (Myrberget 1986b, a, Hannon et al. 1988, Fletcher et al. 2013), this suggests that the relationships found between warm spring weather, early breeding and larger clutches (Paper II), reflect general features for willow ptarmigan populations across areas of similar environmental conditions.

Box 2: High similarities in timing and clutch size responses between study areas

I explored variation in timing of reproduction and clutch size in the study areas in Lierne and Dovrefjell. Using linear models, I modelled the start of incubation for individual female willow ptarmigan as a response of mean temperature during May, measured at the nearest meteorological station (www.met.no) in each study area. Further, I modelled how clutch size is related to the start of incubation. The results show very similar responses between the two study areas (Fig. B2), where high May temperatures advanced the start of incubation (β_{Lierne} = -1.59, CI [-2.12, -1.07]; $\beta_{\text{Dovrefjell}}$ = -1.03, CI [-1.56, -0.50]), which in turn was related to increased clutch sizes (β_{Lierne} = -0.12, CI [-0.18, -0.07]; $\beta_{\text{Dovrefjell}}$ = -0.13, CI [-0.16, -0.10]). There was no clear direct relationship between May temperature and clutch size in either area. May temperatures varied considerably over 7 years in Lierne during 2015-2021 (coefficient of variation (CV): 0.43), and less over 17 years in Dovrefjell during 1978-1994 (CV: 0.34). Variation of incubation start day and clutch size was similar in the two areas ($CV_{\text{Incubation start day}}$: 0.04, $CV_{\text{Clutch size}}$: 0.19, in both areas).

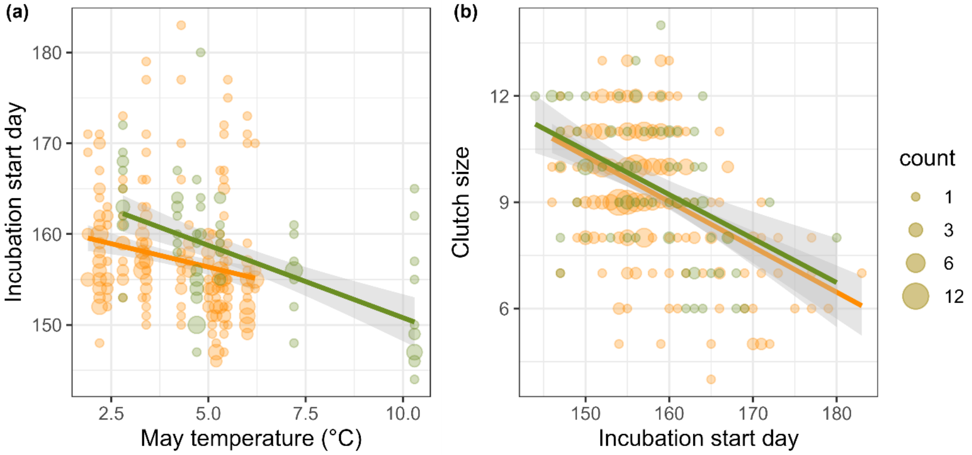

Figure B2: Model predictions based on nesting data from the two study areas, Lierne (green) and Dovrefjell (orange), including renestings. (a) The relationship between the mean of daily temperatures during May and incubation start (day of year, 1 Jan = day 1). (b) The relationship between incubation start and clutch size. Points show raw data and ribbons show 95% CI.

In both our study areas there was high variation among individuals in timing of egg-laying and in clutch sizes (Paper II, Box 2), that was not explained by the climatic variables included in the models. It must be assumed that the factors shaping variation in individual reproductive strategies also include other factors, such as individual heterogeneity (Paper II, Wiebe and Martin 1998a) or experience from previous reproductive events. Similar responses to climatic cues can be assumed to be the main driver of temporal synchrony in breeding (Ims 1990, Youngflesh et al. 2023). Insects are a highly important food source for newly hatched willow ptarmigan chicks (Spidsø 1980), thus, the time of chick hatching should be aligned with the main insect peak to avoid a phenological mismatch (Visser and Gienapp 2019). However, individuals must decide how resources are allocated between growth and reproduction, which may give variation in timing of reproduction among individuals. As spring temperature is related to maternal body mass (Paper II), spring temperature could be expected also to affect variation in timing of breeding among individuals. I found that spring temperature was positively related to breeding synchrony in the Dovrefjell study population (Box 3). Due to this, I speculate that when there are favorable conditions, most individuals are able to breed early. In the opposite situation, when conditions are not favorable, variation in breeding time increases, possibly because breeding time strategies are more affected by individual characteristics. Based on this, I would expect higher breeding synchrony for willow ptarmigan with warmer spring temperatures in the future. According to my findings, early breeding is associated with increased reproductive success (Paper II, Box 2), but it also comes with a risk of a phenological mismatch if the change in breeding time does not match the change in insect development (Visser et al. 1998, Both et al. 2009, Dunn and Møller 2014, Visser and Gienapp 2019). Further, although the main driver of synchrony is climatic cues and matching the insect peak, breeding synchrony may also be a predator avoidance strategy (Ims 1990). Given the importance of the species in many northern mountain ecosystems, this may potentially give cascading effects to the ecosystem. For instance, the specialist predator gyrfalcon preys intensively on willow ptarmigan during the pre-breeding period (Nielsen and Cade 2017). A higher breeding synchrony in willow ptarmigan populations may thus affect the gyrfalcon's availability of food during spring, potentially leading to a shorter and sharper food peak instead of a long-term lower peak.

Box 3: Spring temperature and breeding synchrony in Dovrefjell

Based on the assumption that cold springs would lead to late breeding, and late breeding has been found to increase breeding synchrony in other species (Smith et al. 2010), I predicted that breeding synchrony in willow ptarmigan would be higher in colder springs. I applied an individual-based synchrony index (Kempenaers 1993) for assessing variation in breeding synchrony among the 17 years of the study:

$$SI = \frac{1}{F}\sum_{p=1}^{F}\left[\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p(F-1)}\right]$$

where SI is an index value indicating average proportion of females that are fertile per day over the fertile period and F is the total number of females, $f_{i,p}$ is the number of females, excluding female p, that is fertile on day i, and t_p is the number of days female p is fertile. Following Kempenaers (1993), the fertile period for each female was assumed to start five days before the first egg was laid and to end the day before the last egg was laid. I logit-transformed the response to achieve a normal error distribution and analysed the data using linear models, with climatic windows of mean temperature and snow depth over 15, 30, 45 and 60 days prior to the median date of initiating egg-laying (cf. Paper II) as explanatory variables. In contrast to my expectations, I found that breeding synchrony was higher under higher spring temperatures. The relationship was best explained by a 15 day temperature average (β = 0.12, CI [0.02, 0.21]; Fig. B3). As higher temperature advances breeding time (Paper II), the result suggests that most individuals were able to breed early when there were favorable conditions, and that the variation in individual timing of reproduction increased when conditions were unfavorable.

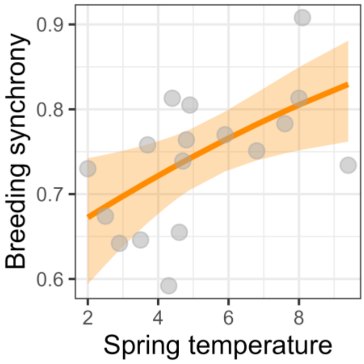

Figure B3: The relationship between spring temperature (°C) over 15 days and yearly breeding synchrony for female willow ptarmigan, with 95% CI. The response was backtransformed before plotting.

Partial migration

Willow ptarmigan in the study population in Lierne was partially migratory, where a part of the population migrated between different areas of the same mountain region (Paper III). The decision to migrate or not was related to juvenile body mass, where heavier juvenile females had higher probability of remaining resident. There was no effect of body mass on the propensity to migrate for adults, and the high level of repeatability in migration strategy suggests that the strategy chosen the first year becomes part of the individual life history as a fixed strategy for later years. We did not model migratory decision in relation to climatic variation among years. However, as juvenile body mass is generally low (West and Meng 1968), and the timing of arrival of winter can be hypothesized to affect the accumulation of resources (Paper IV), climatic variation may indirectly affect variation in migratory decision. If an early arrival of winter leads to lower body mass in the following seasons as discussed in Paper IV, this can be hypothesized to affect the probability of migrating between the winter and summer seasons and should be investigated further. There may also be direct effects of climatic variation on migratory decision. For instance, snow depth may act as a signal of how early nest locations would be accessible, and an early start of the nesting period is associated with increased reproductive success (Paper II, Box 2). Thus, variation in snow depth among years may potentially lead to variation in individual probability to migrate. Further analyses should also investigate variation in climatic parameters between departure and arrival areas. If weather conditions affects migration strategy in willow ptarmigan, this could indicate that phenotypic plasticity exists as a strategy to escape from climatically unfavorable conditions. Although we found no effect on reproductive success from migratory decision, a recent meta-analysis (Buchan et al. 2020) showed consistently higher fitness in resident birds in partially migrating populations. However, the fitness effects showed in Buchan et al. (2020) were generally caused by variation in survival between resident and migratory individuals. I did not investigate to which extent survival was different for resident vs migratory individuals in our study population.

Survival

I examined variation in mortality risk related to variation in snow conditions during spring and autumn (Paper IV). I found that an early arrival of winter imposed a delayed increase in mortality risk for juveniles in the following spring. This carry-over effect may be caused by a limited access to nutrient-rich food after the arrival of winter, affecting the accumulation of resources available for the winter season (Varpe 2017). As juveniles have a greater need than adults for gaining weight during the first autumn (West and Meng 1968), they are likely to be more affected by a reduced access to food resources than adults, which could explain the lack of an effect on mortality risk for adults. We did not have data on juveniles in their first autumn, thus, I could not investigate direct effects of arrival of winter on juvenile mortality risk during autumn. A previous study on willow ptarmigan (Henden et al. 2020) concluded that mortality increased when winter arrived late, as the birds were assumed to experience an increased predation risk in autumn due to a camouflage mismatch between white plumage and lack of snow. Although this appears in contrast to my results, Henden et al. (2020) based their analyses on time series data on ptarmigan abundance sampled in August each year, not data from individual birds. Thus, if a late arrival of winter has a direct negative effect on mortality during autumn due to increased predation risk (Henden et al. 2020), the individuals who are not predated will still take advantage of easier access to nutritious food without snow covering the ground. Consequently, a late arrival of winter could give a delayed decrease in mortality risk during spring for the surviving individuals (Paper IV). Such competing risks between predation hazard and starvation due to limited access to food resources may partly explain the apparent lack of consistency between previous studies (Bowler et al. 2020, Henden et al. 2020, Melin et al. 2020).

I also found variation in spring mortality risk due to spatial variation in snow depth. For both yearlings and adults, spring mortality risk increased with snow depth (Paper IV). The same competing risks can be assumed for the spring season as for the autumn, where the risk of predation due to a camouflage mismatch (Melin et al. 2020) may work in the opposite direction as the risk of starvation. However, the connection between snow depth and access to food resources may be particularly important during spring, as body mass reserves are low after the winter (West and Meng 1968), and there is a need for building up energy stores prior to reproduction (Moss et al. 1975). Lower temperatures and more snow generally leads to a delayed plant greening (Rixen et al. 2022). Thus, it can be hypothesized that due to a lower availability of nutrient-rich buds and shoots in late springs, risk-taking behavior may increase, which eventually could lead to an increase in mortality risk as found in my studies (Paper IV).

Conclusions and future prospects

In the work contributing to this thesis, I tested hypotheses regarding reproduction, migration, and survival in a mountain bird species, with focus on the effects of climatic variation. An overview of relationships I found between climatic parameters and life history traits is shown in Fig. 8. Trade-offs between life history traits are likely to have affected the relationships. For instance, climatic variation during spring was related to both survival (Paper IV), reproductive strategies (Paper II, Box 2) and reproductive success (Paper I), suggesting that trade-off decisions influenced the allocation of resources between reproduction and survival (Wingfield et al. 2017).

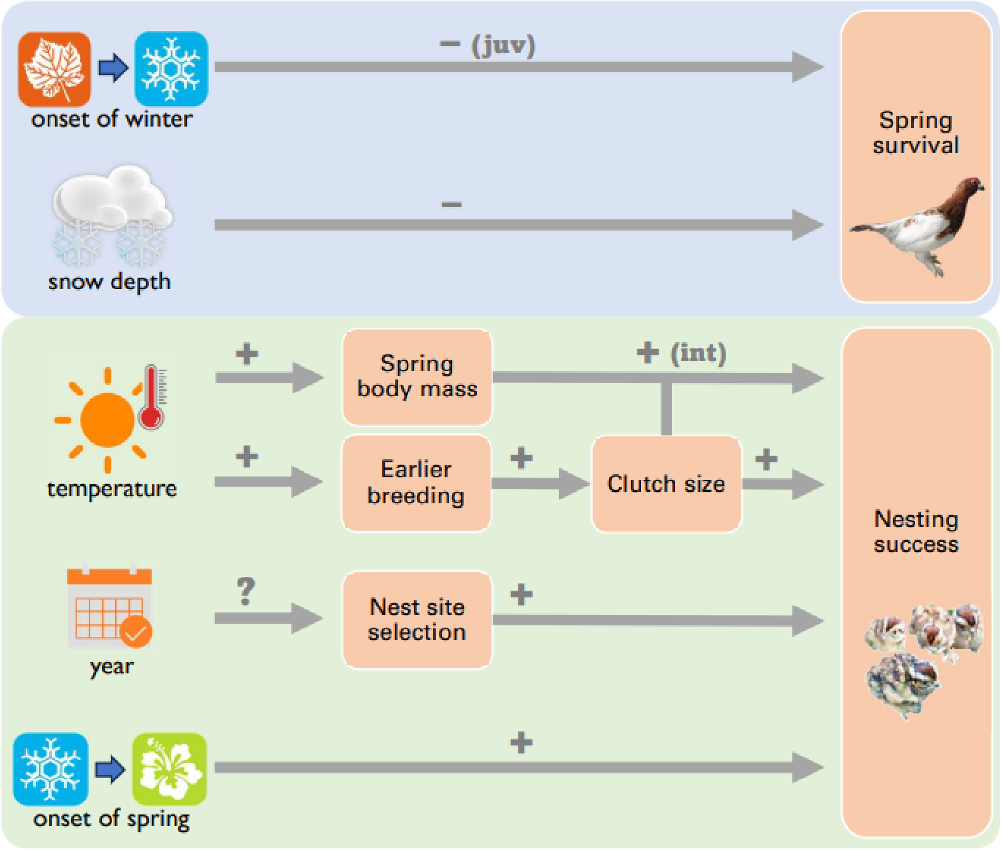

Figure 8: Overview of relationships, found in Papers I-IV, between climatic parameters and life history traits for willow ptarmigan. Plus/minus sign denotes the direction of the effect (juv = juveniles, int = interaction). Nesting success is measured as at least one chick hatched, or as number of chicks hatched (when applicable). Cf. Papers I-IV for details.

Juvenile survival from post-fledging until the first breeding is highly variable between years and an important determinant on population dynamics (Steen and Erikstad 1996, Sandercock et al. 2005). As juvenile mortality risk was affected by variation in snow depth and arrival time of winter (Paper IV), we could expect that snow depth and arrival time of winter also affect population dynamics. In addition to juvenile survival, the pooled offspring survival from egg-laying to four weeks after hatching strongly affects population dynamics (Steen and Erikstad 1996). However, due to a limited amount of data on chicks during summer, I could not investigate if climatic variation affected chick survival. Thus, it is unclear if the increased reproductive investment and success that I found in warmer springs had an effect on recruitment rates in the study populations, although associations between warmer springs and higher population growth rates have been found in other willow ptarmigan studies (Kvasnes et al. 2014, Bowler et al. 2020).

In addition to increasing mean temperatures, also an increased variation around the mean temperatures may affect population dynamics (Lawson et al. 2015). Higher mean spring temperatures lead to earlier breeding (Paper II, Box 2), but earlier breeding might come with a risk of severe weather incidents (e.g., renewed snow cover) that may affect offspring survival (Lehikoinen et al. 2009, Martin et al. 2017, Chmura et al. 2018). A visualization of temperature variation in Dovrefjell over 50 years (Box 4), indicates that mean spring temperatures have increased ($\beta = 0.03$, CI [0.01, 0.05]), while mean temperatures in the 10-day period after the predicted hatching dates have remained constant. However, the minimum recorded temperatures after the hatching dates indicate a weak decreasing trend ($\beta = -0.03$, CI [-0.08, 0.02]). This estimated temperature decrease has notable uncertainty, but it may possibly leave the chicks more vulnerable to hypothermia and starvation (Aulie 1976, Pedersen and Steen 1979, Erikstad and Spidsø 1982, Erikstad and Andersen 1983); ambient temperatures lower than 5-6°C severely affect the feeding opportunities of willow ptarmigan chicks (Erikstad and Andersen 1983), and temperatures around the freezing point have been hypothesized as a limit for being able to obtain food (Pedersen and Steen 1979).

To assess the vulnerability of a species to climate change, we need information about the species' exposure and sensitivity to the changes, as well as adaptive capacity (Dawson et al. 2011). When species are both exposed to and sensitive to climatic changes, the alternative outcomes are often described as 'adapt, move or die' (Dawson et al. 2011). The mountain ecosystems where my study species resides are highly exposed to climate change (Pepin et al. 2015, Adler et al. 2022), and my research shows that willow ptarmigan are sensitive to climatic variation in terms of both survival and reproduction (Papers I, II, IV). Further, it displays adaptive capacity in terms of adjusting the time of reproduction, and it is capable of at least short-distance migrations in response to seasonal variation in the environmental conditions. The results from this doctoral work generally seem to point in a positive direction for the study species; earlier and warmer springs increase reproductive success, and a later arrival of snow in the autumn and less snow in the spring increase survival prospects. This is all in line with ongoing and projected climate change (Callaghan et al. 2011, Adler et al. 2022). As such, isolated relationships between short-term climatic variation and life history traits may apparently suggest that willow ptarmigan is a 'climate winner', but such conclusions should be made with caution, for several reasons. For instance, multiple climatic factors work simultaneously and may interact with each other (e.g., the effects of temperatures above or below the freezing point in combination with precipitation; Peeters et al. 2019). Further, there may be indirect effects through interspecific interactions or cascading effects (Parmesan 2006, Terborgh and Estes 2010). Climatic changes may, for instance, improve access to the mountains

Box 4: Temperature variation over 50 years in Dovrefjell

Climate change leads to overall increased temperatures, but both the effects and the temperature variation may differ between periods of the year. To explore temperature changes in the study area in essential periods for willow ptarmigan reproductive success, I used temperature records from 1970-2020 at the Fokstugu weather station near the study area. To visualize long-term changes in spring temperature, I averaged temperatures over April and May each year (Fig. B4a). Then, based on the spring temperatures and the results from Paper II, I predicted a mean date for chick hatching for each year. I then averaged temperatures over the following ten days (Fig. B4b), to estimate the mean temperature for the time before chicks reach homeothermy and are most vulnerable to low ambient temperatures (Aulie 1976, Pedersen and Steen 1979). Finally, I plotted the minimum temperature that was recorded during the same ten days (Fig. B4c). This extrapolation based on the results from Paper II, suggests that (a) spring temperatures have increased notably in the study area over 50 years (β = 0.03, CI [0.01, 0.05]), likely advancing the breeding time (Paper II), but that (b) mean temperatures during the initial chick period seem to have remained stable. However, (c) the minimum recorded temperature in the same period indicates a weak decreasing trend (β = -0.03, CI [-0.08, 0.02]), with potential negative effects for chick viability (Erikstad and Spidsø 1982).

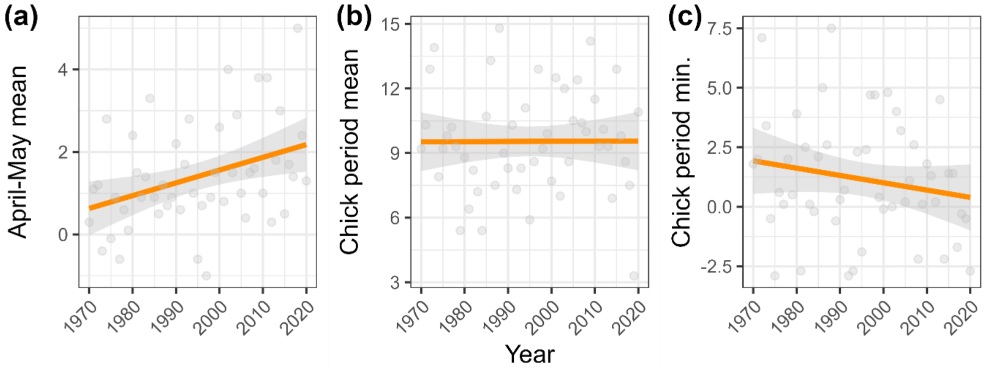

Figure B4: Recorded temperatures (°C) in Dovrefjell in the period 1970-2020. (a) Mean temperature for April and May. (b) Mean temperature for the 10-day period after hatching (predictions based on Paper II). (c) The lowest recorded temperature during the 10-day period after hatching. Orange line shows the linear model with 95% CI.

to a higher number of predators (Elmhagen et al. 2015), affect the insect community (Renner and Zohner 2018, Wagner 2020, Harvey et al. 2023), or change the effects of bacteria or parasite load (Robinson et al. 2019, Ytrehus et al. 2021). Also important to consider, is that the same climatic factor may give different age-specific effects on vital rates (Coulson et al. 2001), contrasting effects in different seasons (Varpe 2017), and contrasting effects on survival and reproduction (Paniw et al. 2021, Canonne et al. 2023). Pacifici et al. (2017) suggested that more than 40% of threatened bird species may have had mixed responses to past climate change, meaning that they have had both negative and positive responses in one or more demographic parameter across a species' range. In conclusion, these aspects may be further investigated with integrated approaches (e.g., Merow et al. 2014, Plard et al. 2019), where the effects of climatic factors are investigated on multiple demographic rates and in different life stages simultaneously (Paniw et al. 2021), preferably over large spatial scales (Pacifici et al. 2017), and including effects of interspecific interactions (Parmesan 2006). This may further extend our knowlegde on how climatic factors affect life history trade-offs, population dynamics and ecosystems, and will aid us in guiding policies for species conservation and management in the future.

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PAPER I

Nest site selection and nesting success under climatic variation in willow ptarmigan *Lagopus l. lagopus*

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PAPER II

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Research

Climatic forcing and individual heterogeneity in a resident mountain bird: legacy data reveal effects on reproductive strategies

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Optimization of clutch size and timing of reproduction have substantial effects on lifetime reproductive success in vertebrates, and both individual quality and environmental variation may impact life history strategies. We tested hypotheses related to maternal investment and timing of reproduction, using 17 years (1978–1994) of individual-based life history data on willow ptarmigan (*Lagopus l. lagopus*, $n = 290$ breeding females with $n = 319$ breeding attempts) in central Norway. We analysed whether climatic variation and individual state variables (age and body mass) affected the number of offspring and timing of reproduction, and individual repeatability in strategies. The results suggest that willow ptarmigan share a common optimal clutch size that is largely independent of measured individual states. While we found no clear direct weather effects on clutch size, higher spring temperatures advanced onset of breeding, and early breeding was followed by an increased number of offspring. Warmer springs were positively related to maternal mass, and mass interacted with clutch size in production of hatchlings. Finally, clutch size and timing of reproduction were highly repeatable within individuals, indicating that individual quality guided trade-offs in reproductive effort. Our results demonstrate how climatic forcing and individual heterogeneity in combination influenced life history traits in a resident montane keystone species.

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THE ROYAL SOCIETY
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1. Introduction

1.1. General introduction

Ongoing climate change will induce variation in individual life histories of vertebrate populations, which in turn will lead to perturbations in the population dynamics of single species that cascade through the foodweb [1]. Climate directly and indirectly affects abundance of food resources and therefore interferes with individuals' energy budgets and influences both acquisition and allocation of resources to growth, self-maintenance or reproduction [2]. For birds, maximizing fitness depends on an optimal investment in clutch size and timing of reproduction (e.g. [3,4]). Clutch size variation within a population is common, and climate-driven resource availability may affect the number of eggs laid [5]. In general, variation in number of offspring is often assumed to be closely linked to variation in food availability [6]. However, previous trade-off decisions [7,8] and individual state variables (e.g. age, body condition or social status) can also affect both ability to acquire resources and current allocation of resources [9,10]. As each individual is expected to optimize its own clutch size, a relationship between individual state variables and number of offspring has been predicted [10].

Reproductive output is generally expected to increase with age [11]. Central among the hypotheses explaining age-specific reproductive investment are the 'constraint' and 'restraint' hypotheses [10], and the 'terminal investment' hypothesis [12]. While the 'constraint' hypothesis posits that young birds are constrained in reproductive abilities directly or indirectly (e.g. through foraging abilities or subdominance in competition over territories), the 'restraint' hypothesis posits that young individuals are holding back on reproductive effort to allocate resources to survival or later reproduction efforts. The 'terminal investment' hypothesis predicts an end-of-life increase in reproductive effort, as there will be no need for resources for later reproductions [8,12,13]. Moreover, considerable research has investigated how parental nutritional state may affect reproductive success (e.g. [14]). Access to sufficient quality and quantity of nutrients is central to allocation of resources and may guide trade-offs affecting reproduction [11], including forcing individuals to invest more in survival and self-maintenance than in reproduction when resources are limited [15]. While individual optimization of clutch size indeed has been shown for some species (e.g. [16]), other studies suggest that an optimal clutch size (or litter size in mammals) can be independent of individual state if environmental conditions during the breeding and offspring-rearing period are unpredictable [17].

In addition to optimizing clutch size, fitness also depends on timing strategies. Adjustment of egg-laying date as a response to spring conditions is common in birds (e.g. [18–20]) and has been shown to be state-dependent for many species [21–24]. Such phenological adaptations are assumed to reflect trade-offs involving self-maintenance (fat storage and somatic growth) and reproduction, but also optimizing the number of offspring and ensuring enough time for offspring growth during summer [3]. There is ample evidence of a relationship between phenology and clutch size for many species, where early breeders generally produce more offspring [22,25–27]. However, early breeding may increase the risk of adverse weather extremes, with potential negative fitness consequences [15].

In this study, we test a set of hypotheses about maternal investment derived from several previous lines of research. We used a unique 17-year time series (1978–1994) of individual-based life history data on willow ptarmigan (*Lagopus l. lagopus*) from central Norway. High-latitude alpine systems like this are ideal for assessing trade-offs in reproductive investment, as the harsh environmental conditions induce strong selection pressure. Breeding seasons are relatively short [19], and hatching too early incurs high risks of sudden incidents of low temperatures or renewed snow cover, which can reduce offspring survival [28,29]. Following best practice procedures for confirmatory research [30], we pre-registered the background for the work and the hypotheses [31]. The specific hypotheses and the deduced predictions are described below.

1.2. Common versus state-dependent optimal clutch size

We first conduct a conceptual quasi-replication [32] of a previous study, by testing the optimization model presented by Gaillard *et al*. [17] in a new taxon. In short, the model contrasts two competing hypotheses of clutch size optimization—*common optimal clutch size* versus *state-dependent clutch size*, respectively. As an extension to the original model (figure 1*a*,*b*), we expect an interaction between individual state and weather [33], predicting a stronger state dependence under harsh climatic conditions (figure 1*c*,*d*). Willow ptarmigan in Norway usually lay 8–12 eggs [34,35]. If optimal clutch sizes depend on individual state (figure 1*bi*) or weather conditions (figure 1*ci*), a change in a state or weather variable will change the number of eggs laid. By contrast, if clutch size is independent of measured state or weather variables,

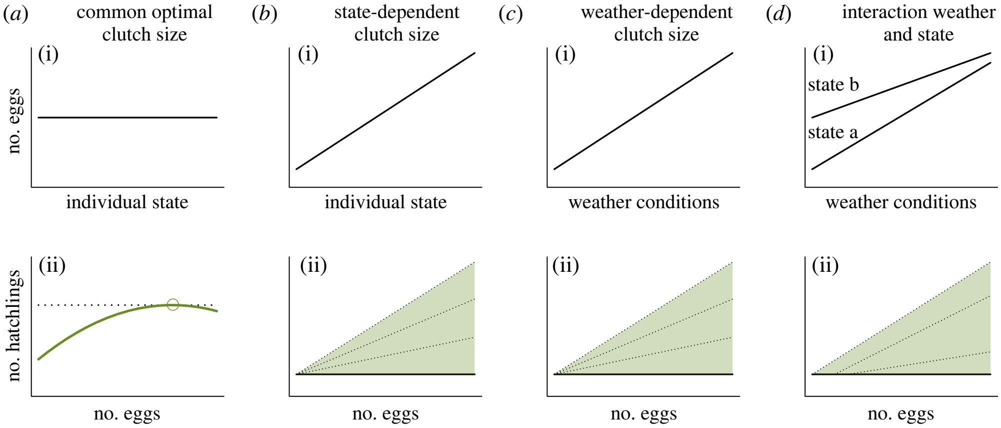

Figure 1. Conceptual representation of the two optimization modes contrasted, *common* (*a*) versus *state-dependent* (*b*) optimal clutch size (modified from [17]). The optimization models are extended with effects of weather (*c*) and interactions (*d*). With a common optimal clutch size, number of eggs is independent from individual state (*a*i) and number of hatchlings will be highest at the most common clutch size (*a*ii). In the case of state- or weather-dependent optimal clutch sizes (*b*i–*d*i), number of hatchlings will increase with clutch size (*b*ii–*d*ii). The filled triangles represent possible reproductive output, limited by the number of eggs laid, and dashed lines inside the triangles show examples of possible slopes depending on the composition of state and weather variables in the population.

there will be no relationship between such variables and number of eggs, suggesting a common optimal clutch size across individuals (figure 1*a*i). We can expect either a positive or quadratic relationship between clutch size and number of hatchlings, and in case of a common optimal clutch size, reproductive output in terms of highest number of hatched chicks will peak at the most common clutch size observed (figure 1*a*ii). If, in contrast, the optimal clutch size is state- or weather-dependent, number of hatchlings will be positively (and linearly) correlated with observed clutch sizes, and number of hatchlings is determined by the composition of important state variables among the individuals, or weather conditions (figure 1*b*ii,*c*ii). Previous studies on subsamples of the data used here found no direct effects of maternal age on clutch size [36,37]. However, it is reasonable to hypothesize that maternal individuals that are young or low on fat-reserves may be constrained (*sensu* [10]) to a higher degree when environmental conditions are stressful [38], potentially affecting both clutch size and number of hatchlings, while older or larger individuals may be more capable to buffer against suboptimal conditions. Body mass has been shown to generally be a good indicator of body condition (i.e. fat content) in birds [39]. Based on the foundation outlined here, we predict that

(i) under the state-dependent model, low maternal body mass leads to reduced number of eggs laid
(ii) under the weather-dependent model, a decrease in local mean spring temperature or an increase in intensity of North Atlantic weather systems (indicated by an increased North Atlantic Oscillation (NAO) index value) is followed by a reduced number of eggs laid
(iii) young females (juveniles, less than 1 year) or females of low body mass are more sensitive to weather conditions than older (adults, greater than 1 year) or larger females, giving an interaction between weather and individual state on number of eggs laid
(iv) a decrease in local mean spring temperature or an increase in the NAO index is followed by a reduced number of hatchlings. This effect will be stronger for young females or females with low body mass

1.3. Onset of spring effects on timing and reproductive success

Onset of spring is expected to affect the timing of reproductive events, and general theory suggests that individuals with higher body mass [23,40] or higher age [38] may initiate egg-laying earlier. Young or low-weight females are expected to be more sensitive to climatic conditions than older or larger females (see also *predictions iii* and *iv*), due to a higher need for self-maintenance and accumulation of body fat before initiation of reproduction. Further, as indicated by Erikstad *et al.* [36] (based on the first 6 years of data) and a wide array of previous studies (e.g. [25,26,38,40,41]), early egg-laying is likely to be positively associated with reproductive output. Thus, we predict that

(v) early onset of spring resulting from higher spring temperatures or early snow-melt will be followed by early egg-laying
(vi) heavy females lay eggs earlier
(vii) adult females lay eggs earlier than juveniles
(viii) young or low-weight females have more delayed egg-laying under harsh climatic conditions than older or larger females
(ix) females that initiate egg-laying early lay more eggs
(x) females that initiate egg-laying early produce more hatchlings

Maternal nutrition is likely to affect reproduction for willow ptarmigan [42,43]. As body mass reserves used for reproduction to a large extent are accumulated from plants consumed in the weeks prior to reproduction [42,44], we predict that

(xi) females will be heavier in springs with high temperatures

1.4. Effects of individual quality beyond measured traits

The concept of ‘individual quality’ has seen different applications in the literature [45,46]. In the current study, we interpret quality as an unmeasured individual life history trait (or an abstract composite of several unmeasured traits), that may act on reproductive success directly or indirectly through other traits. Individual quality is assumed to influence variation in timing of breeding, which in turn is a major determinant of breeding success [23]. Thus, we expect that variation in reproductive success can be partially explained by individual characteristics beyond measured states and therefore predict that:

(xii) females repeat individual strategies with regard to timing of reproduction and number of offspring in consecutive breeding attempts

2. Materials and methods

2.1. Study system

Willow ptarmigan is a medium-sized (400–800 g depending on sex and season) resident tetraonid in Arctic and sub-/low-alpine tundra, with a circumpolar distribution [47,48]. They are relatively short-lived, with only a small proportion surviving to 4 years of age [38], although some individuals survive at least to the age of seven (unpubl. data from Norway; L.F.E. and E.B.N.). Females typically start breeding as yearlings [38], and the role of males in breeding after mating is mostly limited to predator defence [49]. Willow ptarmigan is a precocial species, but chicks are depending on their mother for thermoregulation and predator defence for several weeks after hatching [49,50]. The late winter diet is mainly based on twigs and buds from trees and shrubs, while the spring diet consists of field-layer plants where bilberry (*Vaccinium myrtillus)*, cottongrass (*Eriphorum* spp.), dwarf birch (*Betula nana*) and willows (*Salix* spp.) are central components [43]. The data for this study was collected in a sub-alpine to alpine area (900–1200 m.a.s.l.) of approximately 30 km^2 on the eastern borders of Dovrefjell-Sunndalsfjella National Park in Norway (62°17′N, 09°36′E), in the years 1978–1994. The study area consists of two sub-areas that are divided by a paved road but otherwise connected and undistinguishable. See Pedersen *et al*. [51] for a detailed description of the study area.

2.2. Data collection

We used data from detailed monitoring of reproducing female willow ptarmigan during the breeding season (May–July) in the years 1978–1994. Although field effort was fairly equal between years, the number of females located varied, mainly caused by population fluctuations. We have no reason to believe that individuals nested prior to the start of monitoring. The females were found in mapped territories (cf. [51]) and by searching for clocker droppings (i.e. relatively large deposits of scat left by incubating hens when they occasionally leave the nest). The area was then searched using pointing dogs and beating the bushes with long sticks, trying to flush the incubating female. When nests were detected, females were captured on the nest using throw-nets. Birds were weighed to the nearest 5 g, and age group (juvenile, less than 1 year; adult, greater than 1 year) was determined based on pigmentation of the 8th and 9th primaries [52]. All birds were ringed with metal leg rings and some

Table 1. Weather parameters used to analyse the relationships between climatic forcing, individual characteristics and reproductive success. 'ind/gen' indicate if the weather parameter is calculated according to the breeding dates for each individual bird (ind), or if it is based on a common general time period (gen) with the median laying date of first egg for initial clutches over all individuals and years (i.e. 27 May) as end-date. All temperature (°Celsius) and snow depth (mm) parameters are arithmetic means of the daily means over the time-window.

abbr.	parameter	ind/gen	time period
$\text{Temp}_{\text{pre-ovi}}$	pre-oviposition temp.	ind	1–21 days prior to first egg laid
$\text{Temp}_{\text{pre-inc}}$	pre-incubation temp.	ind	1–21 days prior to incubation start
Temp_{inc}	incubation temp.	ind	21 days of incubation
$\text{NAO}_{\text{May–July}}$	North Atlantic Oscillation	gen	seasonal NAO for May–July
$\text{Snow}_{\text{spring}}$	spring snow depth	gen	15, 30, 45 and 60 days prior to median laying date
$\text{Temp}_{\text{spring}}$	spring temp.	gen	15, 30, 45 and 60 days prior to median laying date
$\text{Temp}_{\text{multiple}}$	spring temp. (multiple)	gen	exploratory approach including all periods in tens 1–60 days prior to median laying date (e.g. 1–10, 1–20, 11–20 days etc.)

individuals were instrumented with a radio transmitter (not part of the present study). Initiation of incubation for each female was estimated by performing flotation tests on eggs [53] and clutch initiation dates were estimated by assuming that after the first egg was laid the female laid one egg per day continuously [54]. As willow ptarmigan incubate for approximately 21 days after laying the last egg [40,55], monitoring of the nest until expected hatching further improved the estimation of oviposition and incubation start dates. Number of eggs in the nest was counted at the time of capturing the female. Number of hatched chicks leaving the nest was estimated as number of eggs, minus number of unhatched eggs and dead hatched chicks found in the nest. Predation events could be separated from hatching by inspecting the eggs, as predators either damaged or removed the eggs while pipped eggshells signified hatched chicks. Similar to Kvasnes *et al*. [56], we defined different time periods during spring-summer where weather is expected to be important for reproductive success. To investigate detailed mechanisms, we defined *individual-based* periods according to the specific dates for each single nest, including a pre-oviposition, a pre-incubating and an incubating period. Following the length of the incubating period [55], all three periods were set as 21-day intervals, and the periods were not used simultaneously in any analyses. In addition to the individual-based weather periods, we used seasonal time-windows of spring temperature and snow depth, based on the median laying date of first egg for initial clutches over all individuals and years, to reveal *general* effects of onset of spring. See table 1 for an overview of all weather parameters used. All weather data are publicly available through The Norwegian Meteorological Institute (https://www.met.no/en/free-meteorological-data/Download-services). We used temperature and snow depth data recorded at Fokstua Meteorological Station, *ca* 30 km south of the study area and within the same mountain region. As it is unclear which climatic variables would be most appropriate and the breeding period stretches over May, June and July, we also used the seasonal station-based NAO index for May–July as an alternative long-term climate variable. The NAO indexes are produced by NCAR's Climate Analysis Section based on Hurrell [57] and are accessible from Climate Data Guide (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based).

2.3. Statistical analyses

The data comprised a total of 319 breeding willow ptarmigan females, including 29 females that were monitored in more than one breeding season. Not all data was collected for all individuals or nesting seasons, and observations with missing data in any parameter used for a specific analysis were removed before conducting the analysis. Willow ptarmigan have only one brood per year but may renest if the first nesting attempt is unsuccessful [34,58]. Based on previous research [36,58], we assumed that nests initiated 16 days or more after the first nest of the season was initiated, was a renesting attempt. We used only initial nesting attempts in our analyses, because renests are based on a different resource base and environmental conditions. One observation with 16 eggs (in 1991) in the nest was removed from clutch size analyses as an outlier, as the second largest clutch in the entire dataset was 13 eggs. Correlated variables (age group and weight, several climatic variables and individual timing events) were not included in the same model. To account for weight loss during incubation, we used residual weight from the relationship *'weight~ incubation time at capture'* as a predictor. *Year effects* were included as random intercepts in mixed-effects models (see details for each tested hypothesis below) for optimal clutch size and timing of reproduction, in order to estimate the residual variation caused by correlations within a year (e.g. caused by annual variation in predation pressure or unmodelled climatic effects). We did not include mother ID as a random effect in our main analyses due to few repeated measurements, but we present alternative models with mother ID as a random effect in the last section of electronic supplementary material, appendix A, with very similar results and the same main conclusions. To avoid overfitting, we included only one interaction effect in any model. Continuous predictor variables were standardized before analyses (i.e. scaled and centred by extracting the mean and dividing on the standard deviation) to facilitate comparisons. All modelling was performed with the statistical software R (version 4.2.2; [59]). Model selection was based on sample-size corrected Akaike information criterion (AIC_c) [60], and we considered models with $\Delta AIC_c < 2$ as competing models. Model fit was assessed by inspection of residuals versus fitted values and distribution of random effect intercepts when applicable. See electronic supplementary material, appendix A for expanded general descriptives of the data, R code (with data management code prior to analyses in electronic supplementary material, appendix B), and a step-by-step walkthrough for each analysis.

2.3.1. Testing the optimal clutch size hypotheses (predictions i–iv)

We first analysed the variation in number of eggs in relation to the state variables *age group* and *body mass* and the climatic variables $Temp_{pre\text{-}inc}$ and $NAO_{May\text{–}July}$ (*model 1*, *predictions i–iii*, $n = 154$, figure 1*a*i–*d*i). In the second part of the optimal clutch model, we analysed the variation in number of chicks that successfully hatched, dependent on number of eggs produced (including quadratic effects of number of eggs to reveal any optimal clutch size), the state variables and the climatic variables $Temp_{inc}$ and $NAO_{May\text{–}July}$ (*model 2*, *prediction iv*, $n = 87$, figure 1*a*ii–*d*ii). We included interactions between egg number, state variables and climatic variables, but not interactions with quadratic effects of egg number as this would give added complexity and not directly reflect the hypotheses being tested. Modelling nest success as a binary response indicated no evidence of a relationship between clutch size and nest failure, thus, we analysed number of hatchlings without considering nests that failed completely. Nests or females that had been subjected to experimental manipulation between egg-laying and hatching (not part of the present study, see [61]) were excluded from the analyses. When assessing variation in number of hatchlings, we created a cut-off excluding nests where more than one-third of the eggs did not hatch, as these observations (9.4% of the sample) with excessive reduction in clutch size between eggs laid and chicks hatched was most likely caused by other mechanisms (partial predation, eggs kicked out by the hen or a high number of unhatched/unfertilized eggs) than what we address in this study. The different causes of excessive reduction in clutch sizes were relatively rare events. Accordingly, including these nests would certainly contribute to conceal the ecological mechanisms we address in the present study. Furthermore, they strongly interfered with model convergence and model validation due to excessive variation, thus, we excluded these nests from the hatchling analyses. Dispersion tests using the *DHARMa* package (version 0.4.6; [62]) revealed that our data was underdispersed (both before and after exclusion of nests with excessive variation in the hatchling analyses), meaning that Poisson model assumptions were violated. Consequently, we opted for modelling reproductive output by use of Conway–Maxwell Poisson distribution (a generalization of the Poisson family allowing for both underdispersion and use of random effects) in generalized linear mixed models (GLMMs) with the R package *glmmTMB* (version 1.1.5; [63]).

2.3.2. Testing the optimal timing hypotheses (predictions v–xi)

In order to explain the variation in timing of egg-laying (*model 3*, *predictions v–viii*, $n = 155$), we modelled the effects of individual state (*age group* and *body mass*), onset of spring ($Snow_{spring}$ and $Temp_{spring}$) and additional climatic variables ($NAO_{May\text{–}July}$ and $Temp_{pre\text{-}ovi}$) with Gaussian error distribution in linear mixed models (LMM), using the package *lme4* (version 1.1–31; [64]). To remove the temporal effects on pre-oviposition temperature, we used the residuals from the relationship '$Temp_{pre\text{-}ovi}$*~timing of first egg laid + random intercept of year*' as a predictor instead of raw values of pre-oviposition temperature. We further tested if variation in timing strategy affected the number of eggs (*model 4*, *prediction ix*, $n =$ 182) or hatchlings (*model 5*, *prediction x*, $n = 108$) by the use of GLMMs with Conway–Maxwell Poisson distribution (see above), where individual *time of first egg laid* and *time of incubation start*, as well as their quadratic effects for assessing any optimal timing, were used as fixed-effect variables. When modelling number of hatchlings (*model 5*), we used the same cut-off for excluding nests with excessive reduction in clutch size between eggs laid and chicks hatched as previously described (7.7% of the sample). In *model 6* (*prediction xi*, $n = 164$), we tested the relationship between pre-laying temperatures and body mass using LMMs, including the *number of days incubated* at capture time as a fixed effect to account for weight loss during incubation. With little prior knowledge of which part of the pre-laying period would be most important, we chose an exploratory selection of climatic windows before the median laying date (i.e. 27 May) for initial clutches in our dataset ($Temp_{multiple}$, cf. Table 1).

2.3.3. Testing the individual quality hypothesis (prediction xii)

To test our third hypothesis, we modelled the consistency within individuals by estimating repeatability in *time of first egg laid* (*model 7*, total $n = 172$ where 31 were repeated observations from 15 resampled individuals) and *clutch size* (*model 8*, total $n = 224$, 33 rep. obs. from 16 ind.), for individual females followed over more than 1 year (range 2–3 years) (*prediction xii*). We estimated the adjusted repeatabilities (*sensu* [65]), fitting LMMs with the package *rptR* (version 0.9.22; [66]) while controlling for fixed-effect covariates found to be important in the previous analyses (i.e. covariates from *model 3* for estimating repeatability in timing and *model 4* for repeatability in clutch sizes). Although the clutch size model (*model 8*) is based on count data, which is usually modelled with GLMM's, the data is underdispersed (see above). The package *rptR* is not recommended for modelling underdispersed count data with Poisson distribution [66], but as the clutch size repeatability model (*model 8*) had normally distributed residuals and passed model validation, fitting also this model as an LMM with Gaussian error distribution should be appropriate.

3. Results

3.1. Optimal clutch size

The most commonly observed clutch sizes for initial clutches were 9 or 10 eggs, together accounting for 51.6% of all initial clutches. As expected, initial clutches consistently had a higher number of eggs than renestings (electronic supplementary material, appendix A). Based on model selection guided by AIC_c, we did not find any clear evidence that initial clutch size varied as a function of maternal state (*prediction i* and *iii*) or included weather parameters (*prediction ii* and *iii*) (*model 1*; table 2; full model selection tables are shown in electronic supplementary material, appendix A). Although maternal weight, $NAO_{May–July}$ and pre-incubating temperature were present among the top models, the biological effects were small and there was high parameter uncertainty in all these models. This indicates a common optimal clutch size across individuals, with limited support to *predictions i–iii*. The mean clutch size for all females in all years was 9.7 (95% confidence interval (CI) [9.25, 10.15], range 5–13 eggs).

For our analysis of number of hatchlings under the optimal clutch size hypothesis (*model 2*; table 2), we base our inference on the two highest ranking models. Both these models indicated a common optimal clutch size across individuals, where the number of chicks produced increased with increasing clutch size until reaching a peak, and where the model predicted declining hatching success at clutch sizes higher than the optimum. However, while the relative gain of additional eggs decreased at larger clutch sizes, the data reveal that clutch sizes were still limited to a level well below the potential common optimum (figure 2*a*, where the model prediction peak is not shown as it is outside of the area where data are present). We found no support for *prediction iv* (number of hatchlings affected by an interaction between weather and maternal state). However, in the second-ranked model (table 2), there was an interaction effect between female body mass and the number of eggs laid on the number of hatchlings ($\beta_{eggs} = 0.145$, CI [0.124, 0.166]; ${\beta_{eggs}}^2 = -0.019$, CI [−0.035, −0.003]; $\beta_{weight} = 0.003$, CI [−0.017, 0.023]; $\beta_{eggs \times weight} = 0.019$, CI [0.001, 0.037]), where hens with high weight produced more hatchlings from large clutches than lighter hens did.

3.2. Optimal timing

There was ample variation in timing of breeding among individual willow ptarmigan females over the years, with earliest start of initiating egg-laying at 16 May and latest (initial clutch) at 6 June. All top-

Table 2. Optimal clutch size model selection tables based on AIC$_c$. Top models with ΔAIC$_c < 2$ and null model (intercept only) for each analysis are shown in ranked order. The parameter 'weight' refers to maternal weight at capture. See electronic supplementary material, appendix A for full model selection tables and parameter estimates and confidence intervals (CI) for all competing top models.

model	ΔAIC$_c$	ΔlogLik	weight
1) optimal clutch size: number of eggs			
null model	0.0	0.0	0.22
weight	0.3	0.9	0.19
NAO$_{\text{May–July}}$	1.8	0.2	0.09
Temp$_{\text{pre-inc}}$	1.9	0.1	0.09
2) optimal clutch size: number of hatchlings			
eggs + eggs^2	0.0	54.2	0.12
eggs + eggs^2 + weight + eggs × weight	0.2	56.5	0.11
eggs + eggs^2 + NAO$_{\text{May–July}}$	0.8	55.0	0.08
eggs + eggs^2 + weight + eggs × weight + NAO$_{\text{May–July}}$	1.0	57.3	0.07
eggs + eggs^2 + weight	1.8	54.5	0.05
null model	104.0	0.0	0.00

ranking models suggest a weather-dependent optimal timing (*model 3*; table 3), giving strong support for our *prediction v* (i.e. higher spring temperature was followed by early egg-laying). Models including time periods of 15, 30 and 60 days prior to egg-laying all have merit, where e.g. a mean increase of 1°C over 15 days led to a 0.62 days (CI [−1.136, −0.097]) advance in egg-laying date (figure 2*b*). We found no effects of maternal weight on timing, giving no support for *prediction vi*. Surprisingly, several models showed a clear tendency of an opposite age-dependent effect of what we anticipated in *prediction vii*, where juveniles started egg-laying earlier than adults ($\beta_{\text{age.juv}} = -1.04$, CI [−2.152, 0.086). There were indications of an interaction effect between age group and spring temperature, but notable parameter uncertainties imply no or weak support to *prediction viii* (timing affected by an interaction between weather and maternal state).

In strong support of our *prediction ix*, we found clear evidence of a relationship between timing of breeding and clutch size. The number of eggs laid was best explained by a negative linear relationship with day of initiating egg-laying (*model 4*; table 3; figure 2*c*). The top model indicated a mean reduction of 0.20 eggs for each day egg-laying was delayed ($\beta_{\text{day of first egg laid}} = -0.083$, CI [−0.107, −0.058]). Further, we found a clear relationship between timing of breeding and the number of hatched chicks, giving an equally strong support for *prediction x* (*model 5*; table 3). The simpler model with linear effects of day of first egg laid ($\beta_{\text{day of first egg laid}} = -0.083$, CI [−0.119, −0.047]) indicated a reduction of 0.18 hatchlings per day egg-laying was delayed. Here, also a quadratic relationship with higher parameter uncertainty was supported ($\beta_{\text{day of first egg laid}} = -0.084$, CI [−0.119, −0.050]; $\beta_{\text{day of first egg laid}^2} = -0.019$, CI [−0.041, 0.004]). An F-test showed no evidence of a difference between the variance in first egg laid and last egg laid ($F_{107} = 1.274$, $p = 0.213$).

There was strong support for our *prediction xi* of a positive relationship between pre-laying temperatures and maternal body mass. The variation in body mass was best explained (*model 6*; table 3) by Temp$_{\text{multiple}}$ (11–20 days before the median laying date 27 May), i.e. a 10 day window in the first half of May in our study area and time period, indicating that a 1°C change in temperature was followed by a 5.1 g increase in body mass (figure 2*d*; $\beta_{\text{incubation time}} = -9.067$, CI [−14.601, −3.406], $\beta_{\text{temp.11–20}} = 9.773$, CI [2.524, 16.759]).

3.3. Individual quality

In full support of *prediction xii*, our results show a high level of repeated strategies among the individuals observed over more than one breeding season. Adjusted repeatability (R), controlled for the effects of age group and mean temperature (0–60 days), was fairly high for timing of first egg laid (*model 7*; $R = 0.59$, CI

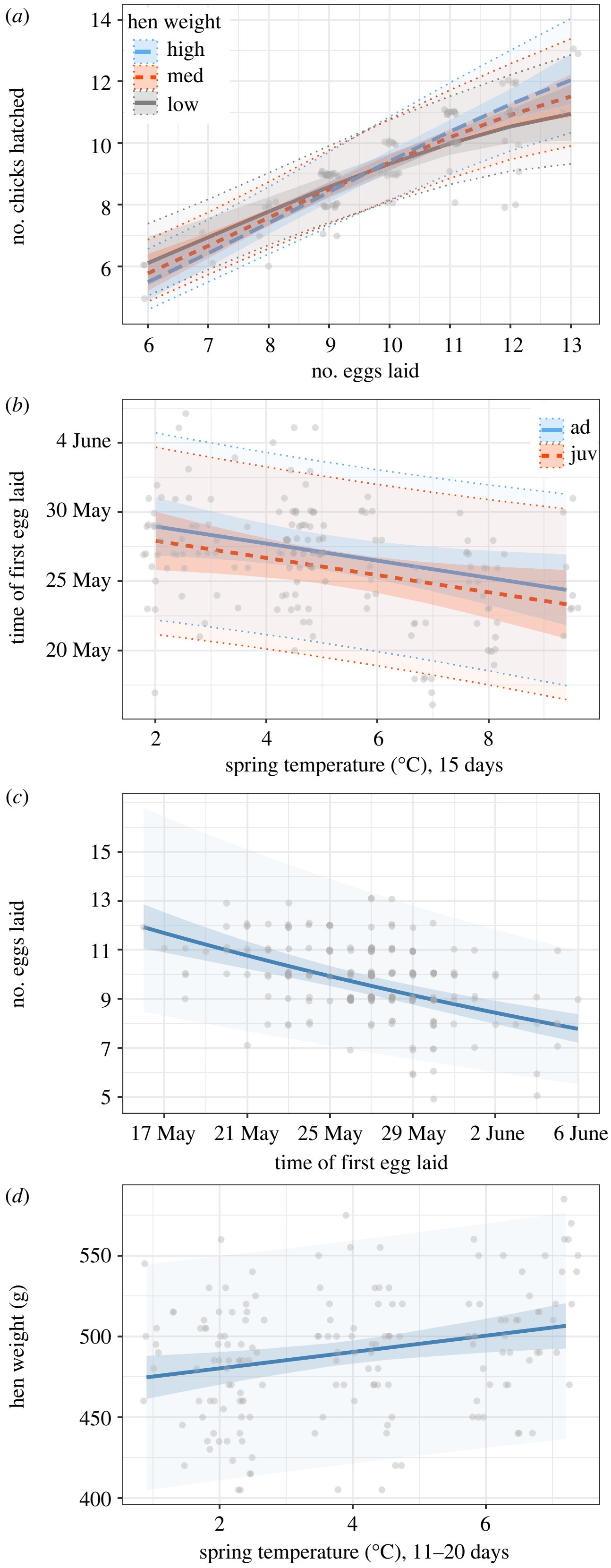

Figure 2. (*Caption overleaf.*)

Figure 2. (*Overleaf.*) The effects of (*a*) clutch size and maternal weight on number of willow ptarmigan chicks hatched (showing the 10th, 50th and 90th percentile of weights), (*b*) age group and spring temperature (over 15 days) on timing of egg-laying, (*c*) timing of breeding on clutch size and (*d*) spring temperature (over day 11–20 before egg-laying) on body mass of incubating females. Densely coloured ribbons are 95% confidence intervals for the population level effects of fixed terms, at the mean values of year as random term. Expanded lighter ribbons are prediction intervals including random year effects. Raw data are shown with jittered points.

Table 3. Optimal timing model selection tables based on AIC$_c$. Top models with ΔAIC$_c < 2$ and null model for each analysis are shown in ranked order. 'Temp$_x$ (days)' indicates the period that mean temperatures are calculated over. See electronic supplementary material, appendix A for full model selection tables and parameter estimates and confidence intervals (CI) for all competing top models.

model	ΔAIC$_c$	ΔlogLik	weight
3) optimal timing: day of first egg laid			
age group + Temp$_{spring}$ (15 days)	0.0	4.4	0.14
age group × Temp$_{spring}$ (15 days)	0.9	5.0	0.09
age group × Temp$_{spring}$ (30 days)	1.0	5.0	0.08
age group + Temp$_{spring}$ (30 days)	1.1	3.9	0.08
Temp$_{spring}$ (15 days)	1.1	2.8	0.08
age group + Temp$_{spring}$ (60 days)	1.4	3.7	0.07
null model	4.6	0.0	0.01
4) optimal timing: number of eggs			
day of first egg laid	0.0	20.2	0.67
day of first egg laid + day of first egg laid^2	1.4	20.5	0.33
null model	38.3	0.0	0.00
5) optimal timing: number of hatchlings			
day of first egg laid + day of first egg laid^2	0.0	11.6	0.55
day of first egg laid	0.4	10.3	0.45
null model	18.8	0.0	0.00
6) optimal timing: body mass			
days incubated + Temp$_{multiple}$ (11–20 days)	0.0	3.1	0.30
null model	4.1	0.0	0.04

[0.31, 0.86]). For clutch sizes, controlled for timing of first egg laid, the level of repeatability was even higher (*model 8*; $R = 0.74$, CI [0.56, 0.89]).

4. Discussion

In the present study, we have demonstrated important relationships between key life history traits and local environmental conditions in a long-term study of a resident low-alpine bird. Using willow ptarmigan as a model species, we tested models of reproductive strategies in relation to individual heterogeneity and climatic variation in a harsh mountanous environment. In our initial analyses, we found no direct effects of maternal state or climatic conditions on clutch sizes. However, when disentangling the different components of reproduction, we found clear evidence that elevated spring temperatures advanced breeding, and strong support for our predictions of increased reproductive output with early breeding. Although the weather effect on timing did not directly influence clutch sizes with our chosen climatic parameters, we see a clear indirect path where temperature modulates breeding time and, consequently, affects reproductive output. Further, we found a positive effect of spring temperature on female body mass, but no direct effect of female mass on breeding time or clutch size, although body mass interacted with clutch size regarding the ability to produce hatchlings. Although Labocha & Hayes [39] found that body mass was an equally good descriptor of body condition (i.e. fat content) as any other index, it is likely to be confounded with structural size to some degree [39], possibly contributing to masking any direct effects of female mass in our results. Our prediction of individual quality was fully supported, with clear evidence of repeated timing- and clutch size-strategies among recaptured individuals.

In the first part of our study, we conducted a quasi-replication of previous work, by testing competing models of optimal clutch size [17] for our model species. The highest ranking model in our model selection procedure was the null model. Thus, number of eggs laid was largely independent of both the included climatic factors (as found for *Lagopus l. scotica* [41], but see Steen *et al.* [33]) and individual state, giving little support to *predictions i–iii*. Although a model including maternal weight was ranked second, parameter uncertainty was substantial. Given the connection between temperature, breeding time and clutch size, it is possible that a wide selection of general weather parameters in our optimal clutch analysis could have returned an apparent direct link between weather and clutch size. However, our focus here was to test hypotheses of detailed mechanisms, thus, we chose to keep our *a priori* set weather parameters.

The lack of clear effects of maternal states on optimal clutch size is in agreement with one previous study on *Lagopus* spp. (*L. l. alexandrae*; [67]) but in contrast with the age effects (*L. l. lagopus*, *L. leucura*; [38]) and weight effects (*L. l. lagopus*; [35], *L. muta hyperborea*; [68]) found by others. The state- and weather-independent clutch sizes in our study may indicate limited physiological costs of egg production, informing a long-standing debate on the matter [69]. It also leads to the assumption of a common optimal clutch size across individuals, in line with the findings for Eurasian lynx (*Lynx lynx*; [17]). As argued by Gaillard *et al.* [17], number of offspring may be independent of maternal state if environmental conditions after breeding are unpredictable, which is the case also for low-alpine willow ptarmigan. However, while the marginal effect of laying one additional egg was reduced at higher clutch sizes, clutch sizes were still confined well below the optimum, i.e. the level yielding the highest output in terms of hatched chicks. This may imply that clutch sizes are limited due to *a)* a time-limitation trade-off to allow sufficient time for chick growth before winter, *b)* territory quality affecting available resources, *c)* a limit on the number of young the parents are able to raise through the summer or *d)* trade-off decisions affecting allocation of available resources to reproduction versus short-term or long-term survival. As willow ptarmigans are able to renest if the initial clutch is lost [58], allowing sufficient time for chick growth is less likely to be the only explanation. Although territory quality has been found to be important for other species (e.g. [70]), Steen *et al.* [71] found no link between territory and food quality in our study population. Regarding a maximum number of young that can be raised, experiments with brood-enlargement show that in most bird species studied, parents were able to raise more young than they had eggs [72]. This is likely to be correct also for willow ptarmigan, being a precocial species, but presumably it is also weather-dependent; although the chicks are self-provided with food, they are dependent on their mother to warm up between feeding sessions [50,73]. Thus, given the unpredictable climatic summer conditions associated with the low-alpine habitat, an excessive number of chicks may increase competition among brood-mates and lead to reduced warming opportunities for the entire brood. Consequently, a bet-hedging strategy [74], i.e. limiting the investment and laying a clutch size below the optimum, may potentially yield the highest reproductive output (e.g. [74]). This strategy is also more resource-conserving than maximizing the clutch size, with potential benefits for long-term reproduction and survival [2]. We do not have data to investigate potential trade-offs between clutch size and future survival or fecundity for the individual chick, but it should be noted that natal brood size could in itself affect individual life histories [75] and, thus, optimal clutch sizes. For example, Spagopoulou *et al.* [75] experimentally demonstrated that collared flycatcher *(Ficedula albicollis)* females from smaller broods had higher reproduction early in life, but faster senescence and higher late-life mortality, than females raised in larger broods.

The analysis of number of hatchlings indicated a common optimal clutch size with interactive effects between number of eggs and maternal body mass. However, we did not find support for the prediction that individual state interacted with weather conditions. It appeared that light-weight females had a lower optimum than heavier females, i.e. the light-weight individuals were less capable of producing a high number of hatchlings from a large clutch size. This indicates that even if light-weight individuals may allocate a relatively higher amount of resources to egg production, the hatching success is reduced compared to heavier females, presumably due to a higher need for foraging during incubation [76].

We found evidence of phenotypic plasticity as female willow ptarmigan adjusted their timing of egg-laying to the onset of spring, supporting *prediction v*. This is in line with the study of Fletcher *et al.* [41] on red grouse (*L. l. scotica*), as well as research on a number of other avian species (e.g. [77]). Plasticity in timing should reflect an ability for the female to accumulate the necessary resources from fresh nutrient-rich plant forage [3,42]. Our results indicate that the weight-increase is most dependent on temperatures in early spring (11–20 days before egg-laying, supporting *prediction xi*), but as female grouse begin gaining weight about a month before egg-laying [42], we can assume that several environmental factors work in concert. Although the ability to adjust timing is state-dependent for many species [22,38,40], we did not see an advancement of breeding due to higher age or body mass (*predictions vi–viii*). Instead, our analyses revealed that juveniles were more than a day *earlier* than adults. That inexperienced females start earlier is particularly interesting as early breeding is followed by a higher number of offspring (supporting our *predictions ix and x*, see also [38,40,41]). We suspect that this is caused by adults showing restraint (*sensu* [10]), possibly based on previous experience of stochastic weather events in the early post-hatching period when harsh weather can severely affect food intake of offspring [29,73]. If this is the case, we see a state-dependent adjustment of timing working in the opposite direction than expected, where the delayed timing may have constituted an adaptation to an increased risk of 'extreme' weather [15].

Individual quality must be assumed to have affected the observed high levels of repeatability in breeding strategies. We found clear evidence for individual consistency in clutch sizes and breeding time, in strong support of *prediction xii*. Our results show a much higher clutch size repeatability ($R = 0.74$) than Myrberget [78] found in a willow ptarmigan population *ca* 850 km northeast from our study area ($R = 0.23$). Also the high repeatability we found in breeding time ($R = 0.59$) is in sharp contrast with e.g. the moderate repeatability in coot (*Fulica atra*) breeding time ($R = 0.32$) found by Perdeck & Cavé [21]. The simultaneous lack of age constraints in our results indicates that the composition of phenotypes in the sample population was probably more important than age distribution for breeding time and clutch sizes, and that individual traits and climatic variation together had great impact on reproductive success.

Our findings suggest that a common optimal clutch/litter size, largely independent of maternal states, may be a general feature across many species breeding and raising offspring in unpredictable environmental conditions. Furthermore, it can be expected that fluctuating climatic conditions in this high-latitude alpine system will result in a fluctuating selection on timing of reproduction and maternal weight, and consequently on clutch sizes. However, an increased risk of stochastic weather events during brooding and chick-rearing as a result of earlier breeding may have adverse effects on the number of juveniles that survive through their first summer [79]. With individual heterogeneity affecting trade-offs involving life history traits such as reproductive rates, this can have direct effects on population dynamics [80]. Accordingly, individual capacity to adapt through plasticity and eco-evolutionary processes is, thus, crucial in the face of climatic changes. We expect this to be a general feature for many species breeding in unpredictable high-latitude mountainous environments, where phenotype composition in meta-populations may be of high importance for the ability to adapt.

Ethics. The ecological data for this study were collected before ethical approvals for wild animal research were issued in Norway. Two of the authors took part in the original field study and state that all applicable guidelines for the use of animals were followed, and that the data were collected responsibly and with animal welfare at highest concern.

Data accessibility. Data used for this article is available from Dryad (https://doi.org/doi:10.5061/dryad.tdz08kq3z) [81]. Weather data are available from https://www.met.no/en/free-meteorological-data/Download-services. NAO data are available from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based.

Supplementary material is available online [82].

Authors' contributions. L.F.E.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft and writing—review and editing; T.H.R.: conceptualization, investigation, supervision, validation and writing—review and editing; H.C.P.: data curation, investigation, validation and writing—review and editing; E.B.N.: conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, validation and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We have no competing interests.

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PAPER III

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RESEARCH ARTICLE

Drivers and consequences of partial migration in an alpine bird species

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Abstract

1. Partial migration, where a portion of the population migrates between winter and summer (breeding) areas and the rest remain year-round resident, is a common phenomenon across several taxonomic groups. Several hypotheses have been put forward to explain why some individuals migrate while others stay resident, as well as the fitness consequences of the different strategies. Yet, the drivers and consequences of the decision to migrate or not are poorly understood.
2. We used data from radio-tagged female ($n = 73$) willow ptarmigan *Lagopus lagopus* in an alpine study area in Central Norway to test if (i) the decision to migrate was dependent on individual state variables (age and body weight), (ii) individuals repeated migratory decisions between seasons, and (iii) the choice of migratory strategy was related to reproductive success.
3. Partially supporting our prediction that migratory strategy depends on individual state, we found that juvenile birds with small body sizes were more likely to migrate, whereas large juveniles remained resident. For adult females, we found no relationship between the decision to migrate or stay resident and body weight. We found evidence for high individual repeatability of migratory decision between seasons. Migratory strategy did not explain variation in clutch size or nest fate among individuals, suggesting no direct influence of the chosen strategy on reproductive success.
4. Our results indicate that partial migration in willow ptarmigan is related to juvenile body weight, and that migratory behavior becomes a part of the individual life history as a fixed strategy. Nesting success was not affected by migratory strategy in our study population, but future studies should assess other traits to further test potential fitness consequences.

KEYWORDS
alpine wildlife, eco-evolution, *Lagopus lagopus*, migration

TAXONOMY CLASSIFICATION
Behavioural ecology

1 | INTRODUCTION

Migration between distinct breeding and wintering areas is a widespread behavioral trait in many species across a wide range of taxa, and is generally assumed to be an adaptation to seasonal variation in environmental conditions (Reid et al., 2018). Such seasonal migrations can increase individual fitness (Alerstam et al., 2003; Somveille et al., 2015), as it allows the birds to utilize highly productive habitats all year-round. In contrast, other bird species do not perform long-distance seasonal migrations, as they are adapted to remain at high latitudes throughout the entire year and survive the low-productive winters (Barta et al., 2006; Svorkmo-Lundberg et al., 2006). However, species that display such behavior may perform shorter migrations between summer and winter areas in heterogeneous landscapes where availability and/or quality of resources vary between seasons (Barraquand & Benhamou, 2008; Fedy et al., 2012). Some overwintering populations are partially migratory (Chapman et al., 2011), implying that a portion of the population migrates between summer and winter areas, whereas the rest stay resident.

Partial migration has received considerable attention in the literature in the last decade (Berg et al., 2019; Chapman et al., 2011; Cobben & van Noordwijk, 2017; Hegemann et al., 2019; Pulido, 2011; Reid et al., 2018), and several hypotheses have been put forward to explain both within-species and within-population variation in migratory behavior. Lundberg (1987, 1988) suggested that the evolution of partial migration could be explained by two alternative hypotheses. First, it could evolve (i) as a frequency-dependent evolutionary stable strategy (ESS) with two phenotypic tactics – or genetic dimorphism with two coexisting morphs (i.e., migrants and residents) – with equal fitness payoffs. Second, partial migration could evolve (ii) as a conditional strategy where individual state variables and interactions with environmental factors determine the decision to migrate or not at the individual level. Moreover, three well-established hypotheses have been put forward to explain the drivers behind partial migration based on individual traits (i.e., conditional strategies; Chapman et al., 2011). These traits can be individual fixed-state variables such as age and sex, or plastic state variables such as body condition (Lundberg, 1988). The body size hypotheses (Hegemann et al., 2015; Ketterson & Nolan, 1976) suggest that large individuals are more likely to stay resident due to higher ability to endure seasonal fluctuations in food abundance and temperature/weather conditions, whereas smaller individuals are more likely to migrate to habitats with more benign environmental conditions. In the traditional form, the body size hypothesis states that large body mass is most advantageous during winter due to higher thermal or nutritious stress in this season (Chapman et al., 2011; but see Alonso et al., 2009). The dominance hypotheses (Gauthreaux, 1982) suggest that dominant (often larger) individuals have a competitive advantage in environments with limited food resources (Mysterud et al., 2011) or nesting sites (Gillis et al., 2008), which could trigger migration in smaller or sub-dominant individuals. The arrival time hypothesis (Ketterson & Nolan, 1976) suggests that because of earlier nest site occupancy and higher fitness of early arriving birds, individuals arriving early at the breeding site have higher reproductive success. Hence, birds that stay in the territory year-round, are expected to have higher reproductive success. In cases where there is intrasexual competition for breeding sites, some individuals might decide to migrate. The body size, dominance, and arrival time hypotheses suggest that the decision to migrate or stay in the area year-round is influenced by individual state, intraspecific interactions, or environmental conditions, and that the fitness reward from the two alternative strategies can differ. These different hypotheses might play out differently in populations where residents and migrants share a non-breeding habitat but breed allopatrically (i.e., *breeding partial migration*) and in populations where residents and migrants share a breeding habitat but live allopatrically during the non-breeding season (i.e., *non-breeding partial migration*; Chapman et al., 2011). So far, most research has focused on non-breeding partial migration, but breeding partial migration has been studied in, e.g., American dippers *Cinclus mexicanus* (Gillis et al., 2008).

The fitness consequences of being resident vs. migratory in a partially migratory population are poorly understood (Berg et al., 2019; Chapman et al., 2011). Nevertheless, differences between resident and migratory individuals in fitness parameters such as survival and reproduction have been suggested in theoretical and reported from empirical studies. Theoretical studies suggest that a conditional strategy can result in unequal fitness between strategies in partially migratory populations (Chapman et al., 2011; Kokko, 2011; Lundberg, 1987, 1988). Most empirical studies also report fitness to differ between migratory strategies (Buchan et al., 2019). For instance, in a partially migratory population of American dippers, Gillis et al. (2008) found that migrants had lower reproductive success but higher survival rates compared to resident individuals. The higher survival rates did, however, not offset the lower reproductivity. Adriaensen & Dhondt (1990) found both higher survival and reproductive success in resident European robins *Erithacus rubecula* and hypothesized that the differences could be attributed to a conditional strategy. In contrast, Hegemann et al. (2015) found no differences in reproductive success between migrants and residents in a skylark *Alauda arvensis* population, despite higher average body mass in resident birds. Both theoretical and empirical studies generally suggest migration to be a losing strategy within partially migrating populations, and that the decision to migrate may be to make “the best of a bad job” (Chapman et al., 2011).

Empirical studies on potential fitness consequences of partial migration have so far been limited to passerines, although partial migration is a common phenomenon reported in multiple bird orders, including Galliformes (Cade & Hoffman, 1993; Chapman et al., 2011; Grist et al., 2017; Holte et al., 2016). The willow ptarmigan *Lagopus lagopus* (Figure 1) is a tetraonid bird with a circumpolar distribution (Fuglei et al., 2020), which lives year-round in heterogeneous alpine and artic ecosystems. Because male willow ptarmigans regularly display polygamy, male breeding success is therefore more difficult to quantify than female breeding success and consequently more often unknown (Tarasov, 2003). Several studies have reported migratory behavior in ptarmigan populations (Brøseth et al., 2005; Gruys, 1993; Hoffman & Braun, 1975; Hörnell-Willebrand et al., 2014; Irving et al., 1967; Nilsen et al., 2020). From Sweden, Hörnell-Willebrand et al. (2014) reported considerable individual variation in seasonal migration distances in willow ptarmigan, with some individuals considered to be residents and others to be migrants. Empirical data from other Scandinavian ptarmigan populations imply non-migratory behavior (Pedersen et al., 2003), suggesting that there are both inter- and intrapopulation differences in the propensity to migrate between summer and winter areas in willow ptarmigan. Willow ptarmigans from some populations often gather in distinct wintering areas (Weeden, 1964), which suggests these populations to be breeding partially migratory (Chapman et al., 2011) due to some individuals migrating to breeding areas during spring while others stay resident, either in the wintering or in the breeding areas. Currently, the drivers and consequences of partial migration in willow ptarmigan are poorly understood.

Here, we test a number of predictions from a preregistered hypothesis (Arnekleiv et al., 2019; Nilsen et al., 2020) put forward to explain causes and consequences of partial migration behavior in female willow ptarmigan. We focused on females only because we did not have access to reproductive success data from males in our study population. Assuming that migrants are making the best of a bad job (Lundberg, 1987), and based on the hypotheses about state-dependent evolution of partial migration in birds outlined above, we predict that:

FIGURE 1 Radio marked willow ptarmigan female. Photo is taken by an automatic game camera mounted at the females nest

1. Female willow ptarmigans with (a) large body size are more likely to remain resident than females with smaller body size, and (b) juveniles are more likely to be migrants than adults.
2. Migration is not a fixed strategy in female willow ptarmigan.
3. Resident female willow ptarmigans have higher nesting success than migrants.

Under the assumption that winter is the most thermally or energetically constraining season as implied in the traditional form of the body size hypothesis (Chapman et al., 2011; Ketterson & Nolan, 1976), our data would not allow for an efficient test of this hypothesis. The body size hypothesis would typically be tested with data from systems with non-breeding partial migration, as defined above. The predictions were preregistered (Nilsen, Bowler, et al., 2020) at the Open Science Framework (OSF) prior to analyzing data (Arnekleiv et al., 2019).

2 | METHODS

2.1 | Study area

The study was conducted in Lierne municipality in the northeastern part of Trøndelag County, Norway, with minor extensions of the study area into neighboring municipalities Snåsa, Røyrvik, and Grong due to longer movements from the main study area by some individuals (Figure 1). Ptarmigans were captured at two sites (Guslia and Lifjellet), which were located 20 km apart near Blåfjella-Skjækerfjella National Park (Figure 2). Both in winter and summer, willow ptarmigans are distributed across the larger study area, and some birds overwinter also in the breeding areas of the migratory birds from this study. Because we only captured birds during winter at two specific capture areas, birds that were resident at other sites in the larger study area would not be available for capture in our study. This also limited our ability to test the body size hypothesis. The study area was situated in the low alpine and north boreal bioclimatic zones (Moen, 1999); the low alpine zone was dominated by *Salix* spp., dwarf birch *Betula nana*, and *Ericaceae* spp. interspersed with birch *Betula pubescens*, whereas the north boreal zone was dominated by Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, birch *Betula* spp., Ericaceae dwarf shrubs, and bryophytes.

2.2 | Field data collection

Willow ptarmigans were captured during February and March during winter 2015–2019. The birds were spotted from snowmobiles during night-time and temporarily blinded with powerful headlamps and caught with long-handled dip-nets (Brøseth et al., 2005; Hörnell-Willebrand et al., 2014; Sandercock et al., 2011). Body weight (measured with Pesola LightLine 1000 g spring scale – rounded to nearest 5 g) and wing length (measured with Axminster Workshop Hook Rule 300 mm – carpal to tip of longest primary

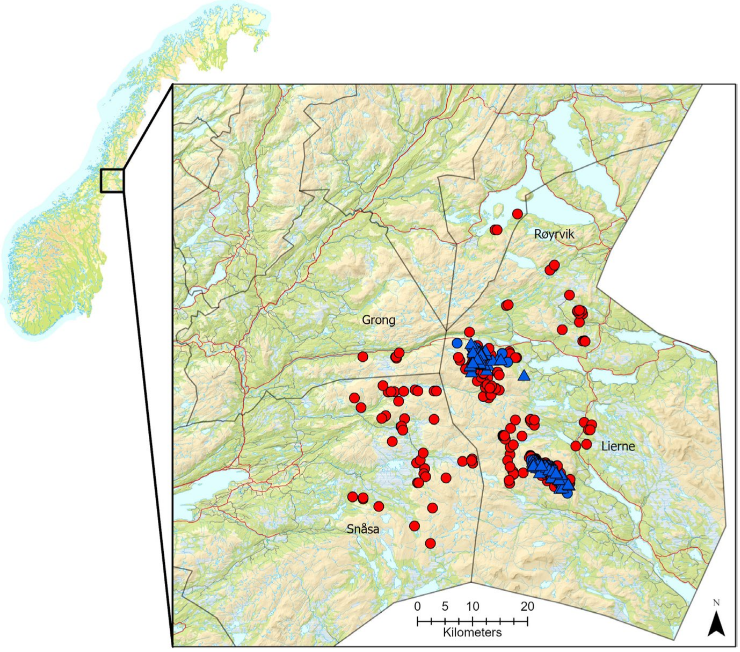

FIGURE 2 Triangulated positions of all female willow ptarmigan during the study period in the winter (January–March, blue circles) and summer (May–July, red circles) seasons. The blue triangles represent capture locations; the northern cluster is Lifjellet capture site and the southern cluster is Guslia capture site. Map to the left shows the location of the study area in Central Norway

of flattened wing, measured to nearest mm) were measured prior to instrumenting the birds with radio collars. Captured birds were identified in the field as either female or male based on saturation of red in the eyebrow, where males have more pronounced red color than females (Pedersen & Karlsen, 2007). One feather was collected for DNA analyses to confirm sex, and the genetic marker Z-054 (Dawson et al., 2015) was used to determine the sex of the bird. Eighty-five percent of the sex assignments in the field were correct (Israelsen et al., 2020). Captured birds were also classified into juvenile (captured during the first winter following the year of birth) and adult (2nd year +) based on the amount of pigments in primary feathers 8 and 9, where juveniles have more black pigments in 9 than in 8 (Bergerud et al., 1963). Each individual was marked with a stainless steel ring with a unique identification number. Most of the birds were equipped with a VHF radio tag (Holohil – RI-2DM, 14.1 g) on the 152 MHz frequency band. For all marked birds, the combined weight of the leg ring and radio transmitter was <3.5% of the body weight. Radio transmitters were programmed to send mortality signals after recording no movement for more than 12 h. In March 2018, five ptarmigans were captured and marked with GPS transmitters (Milsar – GsmRadioTag-S9, 12 g). The transmitters sent position data over the GSM network every 4th hour.

Willow ptarmigan positions were for the most part collected once a month by manual tracking on foot by triangulation, using handheld receivers (Followit – RX98) and antennas (Followit – four-element Yagi-antenna); 2–5 bearings were used to determine best position and the distance between each telemetry location varied from 0.3 to 1 km. If only two bearings were obtained, the cross-section was included when the terrain indicated that the observation was trustworthy (e.g., when the cross-bearing pointed to a position in the end of a valley). Few positions were collected in January and December due to short day length and challenging weather conditions. To avoid loss of data due to long-distance movements, we conducted wider aerial triangulation using a helicopter or fixed-winged airplane three times a year (May, September, and November) in the years 2016–2019. In 2015, we only conducted triangulation from the air in October. Additional positions were either on-site direct observations from captures or homing in on individuals.

Nesting success in spring was first assessed by homing in on radio-tagged females to check whether they were nesting. Furthermore, incubating females were flushed off the nest, eggs were counted, and a wildlife camera (Reconyx HF2X Hyperfire 2 or Wingcam II TL) with movement sensor was deployed 2–5 m from each nest. The nests were revisited in July after hatching to determine the fate of the nest by inspecting and counting the eggshells to see whether and how many eggs were hatched or predated. In addition, pictures from the cameras were examined.

2.3 | Classification of migratory behavior

To examine migratory movements between seasons, we classified January–March as winter and May–July as summer. Of a total of $n = 101$ captured female ptarmigans, only females with data from at least one winter and the consecutive summer season were included in the analysis ($n = 73$) (Table 1). We collected 1–2 positions per individual in the winter and 1–5 positions per individual during summer. For each female in each season, migratory decisions were determined based on whether or not there was overlap between the winter home range and the consecutive summer home range (Figure 3), and between the summer home range and the consecutive winter home range.

Due to the limited amount of location data for each individual, we were not able to use the more data hungry approaches that have been developed for research on GPS-tagged individuals (Cagnacci et al., 2016). Thus, we opted to create a decision rule for classification of migratory decision based on the available data and the assumption that all females shared a common home range size in summer and winter, respectively. We used the following approach:

First, we calculated an average winter home range size from positions of three of the GPS-tagged ptarmigan during the winter 2018, all marked in March 2018. Individual home range sizes were calculated as 95% Minimum Convex Polygons (MCP) using the function *mcp* in R package adehabitatHR (Calenge, 2006). The average 95% MCP for the three GPS-tagged ptarmigans was 4.08 km^2. Before calculating the individual 95% MCPs, we removed inaccurate positions (due to GPS error). We defined a position as an outlier if the distance between two consecutive positions (i.e., time t and $t - 1$, respectively) was more than two times the distance between positions surrounding the focal position (i.e., distance between position taken at $t - 1$ and $t + 1$). Positions from the GPS-tagged ptarmigan were only used to estimate the average "baseline" winter home range size, and these birds were not included in further analyses. For each of the VHF-tagged females included in the analyses, we assumed that they had a circular winter home range equal to the size calculated from the GPS data (4.08 km^2 (radius = 1140 m)) centered around the activity center (determined by triangulation) of each female in each winter season; this was used as a proxy for individual winter home range size and location.

Second, we estimated the size of the summer home ranges using data from VHF-tagged female ptarmigan with ≥3 positions during the summer season (May–July). For each female, we drew a polygon based on the positions, and calculated the area of the polygon. As a measure of a "baseline" summer home range for further analysis, we used the median of all the individual summer home range sizes ($n = 46$). The baseline home range area was estimated to be 0.058 km^2, corresponding to a circular home range with radius = 136 m. This size is in good agreement with previous studies of ptarmigan summer home range sizes (Eason & Hannon, 2003). For each of the females included in the analyses, we assumed a circular summer home range of 0.058 km^2 (radius = 136 m) centered around the activity center (determined by triangulation and nest location) of each female in each summer season, as a proxy for individual summer home range. When calculating the activity center, the activity center for nesting hens ($n = 68$) was shifted toward the nest location, by assigning equal weights to the position of the nest and the sum of all other positions. All spatial computations were done using R (R Core Team, 2019).

Females with overlapping winter/summer or summer/winter home ranges were classified as residents, whereas females with no overlap were classified as migrants. Based on the "baseline" home range sizes, ptarmigans moving further than 1276 m (radius winter home range + radius summer home range) were consequently classified as migrants and females moving less than 1276 m were classified as residents.

TABLE 1 Number of radio-tagged female willow ptarmigan captured in the capture sites Guslia and Lifjellet. *N* observations/nests show the total number of individual migratory decisions and nests included in the analysis of the first spring transitions from winter to summer areas. The numbers in parentheses show number of observations/nests when repeated decisions for some birds, and both spring and autumn movements, were included in the mixed effects models presented in Appendix S1

Year	Guslia	Lifjellet	*N* marked	*N* observations included in analyses	*N* nests included in analyses
2015	14	6	20	14 (14)	10 (10)
2016	10	10	20	16 (23)	13 (14)
2017	8	12	20	14 (24)	6 (7)
2018	4	13	17	11 (20)	11 (13)
2019	11	13	24	18 (23)	16 (18)
Total	47	54	101	73 (104)	56 (62)

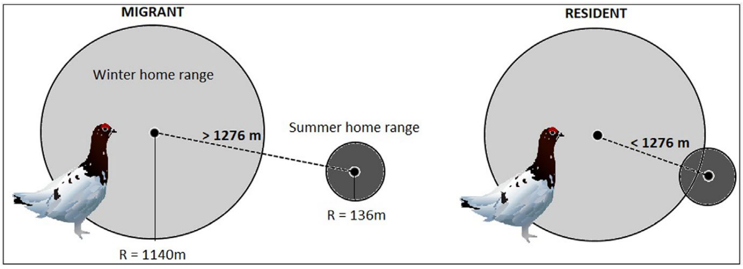

FIGURE 3 Female ptarmigans were classified as either migrants, if the distance between the activity center of winter and summer home ranges exceeded 1276 m (i.e., no overlap), or residents, if the distance between the centroids of winter and summer home range was less than 1276 m (i.e., overlap)

2.4 | Statistical analysis

To test our predictions about state-dependent migration strategy, we used generalized linear models (GLM) based on data from the first spring migratory decision for each bird. Although this limited our sample size, it allowed a more stringent test of the migratory decisions from a sympatric wintering area to allopatric breeding area (i.e., *breeding partial migration*). Migratory decision was modeled as a binary response variable (see above), and body weight, age, and body weight × age interaction as fixed explanatory terms. Body weight was used as a measure of body size. Body weight can, however, fluctuate across short and long time intervals, and such intraindividual variation might make body weight a less reliable measure of body size; we acknowledge this limitation of the current study. For all models, the body weight variable was standardized by extracting the mean and dividing by the standard deviation. Under the assumption that migratory decisions are (relatively) fixed and symmetrical across seasons, we also analyzed the data using generalized linear mixed effects models including all observations (*glmmTMB* function in R package glmmTMB; Brooks et al., 2017), with migratory decision as a binary response variable and bird identity included as random effect to account for repeated observations of individual birds. Note that this approach included both spring and autumn migration decisions. The results from the mixed effects models are presented in Appendix S1.

As an additional test of prediction 1, we also tested whether the distance migrated was influenced by age and body weight by fitting linear models (GLM) with log(movement distance) as response variable, and weight, age, and the weight × age interaction as fixed explanatory terms. We used an identity link function (assuming a Gaussian distribution of the residuals), and included only the first spring migratory decision for each bird. As above, we repeated the analyses including all data (i.e., repeated observations for some birds, and including both spring and autumn migratory decisions), we used generalized linear mixed effects models (*glmmTMB* function in R package glmmTMB), including bird identity as intercept term to account for repeated observations of individual birds.

To assess if the decision to migrate or not was a fixed strategy in female willow ptarmigan, we estimated the repeatability R_M in a mixed-effect model with log(movement distance) as response variable. Only females with two or more observations of seasonal migration decisions were included. We also assessed models for repeatability in migratory decision (binary response), but do not report those due to convergence failure. Repeatability R_M was estimated as the proportion of the total variance that was attributed to within-group (bird identity) variation (Sokal & Rohlf, 1995):

$$R_M = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

Agreement repeatability was estimated based on the intercept-only model (i.e., not accounting for any fixed factors), whereas adjusted repeatability was estimated with age included as a fixed-effect term in the model (Nakagawa & Schielzeth, 2010). Repeatability was calculated using the rptR package (Stoffel et al., 2017), and the 95% confidence interval for the repeatability was estimated using parametric bootstrapping ($n = 1000$).

To test whether reproductive success was influenced by migratory strategy, we (1) fitted generalized linear models with number of eggs as response variable; migratory decision, age, weight, and year as explanatory variables; and bird identity as random effect. Because clutch size data are often underdispersed (Kendall & Wittmann 2010), we used a Conway–Maxwell–Poisson distribution that includes an additional parameter (ϕ) that accounts for violations in the mean-variance assumption in a standard Poisson distribution. The models were fitted to the data from the first spring after capture for each bird using the function *glm.cmp* in package mpcmp (Fung et al., 2020). Then, (2) we fitted generalized linear model with nest fate as binary response variable (i.e., hatched chicks vs. predated or abandoned nest) and migratory decisions, age, weight, and year as explanatory variables and with bird identity as random effect. We repeated the analyses including all observations (i.e., more than 1 year for some birds) using generalized linear mixed effects models (*glmmTMB* function in R package glmmTMB). The results from the mixed effects models are presented in Appendix S1.

All model selection was based on the Akaike's information criterion corrected for small sample sizes (AIC_c) (see, e.g., Bolker et al., 2008). The AIC_c encourages parsimony by adding a term to penalize more complex (larger number of parameters) models (e.g., Bolker et al., 2008).

Data and R-code are available from an open archive hosted by the Open Science Framework (Arnekleiv et al., 2022).

3 | RESULTS

3.1 | Migration strategy in relation to age and body weight

A total of 104 cases of seasonal movement behaviors (i.e., decisions to migrate or remain resident) were included in this study (Table 2), of which 87 were winter area to summer area movements and 17 were movements from the summer area to the winter area. When including only transitions from winter to summer areas, three times as many cases of migratory ($n = 53$, 73%) than of resident ($n = 20$, 27%) behaviors were observed (Table 2). Mean and median movement distances – for both juvenile and adult females – were substantially longer than the distance limit for being classified as migrant (1276 m; Table 3). Overall, 67% of the seasonal movement distances were shorter than 10 km, 25% were between 10 and 25 km, whereas only a few (8%) seasonal movements were longer than 25 km (Figure 4). In general, seasonal movement distances were longer for birds marked at Guslia compared to birds marked at Lifjellet (Figure 3). Mean and median differences in weight between juveniles and adults were small (Table 3). There was no evidence for a difference ($p = .70$ – linear model) in elevation of the nest site locations between residents (mean elevation: 593 m.a.s. ±23) and migrants (583 m.a.s. ±16).

When modeling the decision to migrate or remain resident (including only the first spring movement for each individual female ptarmigan) as a function of age and body weight, we found strongest support for the full model including the age x weight interaction (Table 4, Appendix S1). This is in partial support of our prediction 1. A similar result was found when including all data (i.e., repeated observations for some birds, and both spring- and autumn movements; Appendix S1). The full model received substantially more support than the second-ranked model (Table 4). For juveniles, the probability of migrating decreased with body weight (Figure 5), and thus the probability of remaining resident increased with weight. For adults, there was no apparent influence of body weight on the decision to migrate or remain resident. When modeling movement distance as a function of age and weight (including only the first spring movement for each individual female ptarmigan), we found no support for a difference between juveniles and adults (Table 5, Appendix S1), and the intercept-only model had lowest AIC_c. Similar inference was made when including all observations (i.e., repeated observations for some birds, and both spring and autumn movements; Appendix S1).

3.2 | Repeatability of migratory behavior

Repeatability of migratory behavior within individuals was very high (Figure 6), and repeatability within individuals increased each consecutive season. Among those individuals that changed migratory strategy, some were originally migratory, whereas others were originally resident. Agreement repeatability (based on the intercept-only model) for movement distance revealed very high repeatability ($R = 0.69$, 95% CI = 0.36–0.85). Repeatability was equally high after accounting for potential age effects (i.e., adjusted repeatability) in movement distance ($R = 0.71$, 95% CI = 0.40–0.87).

TABLE 2 Distribution of decisions to migrate or remain resident from winter to summer (first year of data after capture only) observed for 73 female willow ptarmigans during the 5-year study period. The numbers in parentheses include all observations of migratory decisions, both from winter to consecutive summer and from summer to consecutive winter

Year	Residents	Migrants	Total	% Migrants
2015	6 (6)	8 (8)	14 (14)	57 (57)
2016	5 (5)	11 (18)	16 (23)	69 (78)
2017	5 (5)	9 (19)	14 (24)	64 (79)
2018	1 (4)	10 (16)	11 (20)	91 (80)
2019	3 (6)	15 (17)	18 (23)	83 (74)
Total	20 (26)	53 (78)	73 (104)	73 (75)

3.3 | Nesting success

In contrast to our third prediction, we did not find evidence that clutch size (Table 6, Appendix S1) or nest fate (Table 7, Appendix S1) varied as a function of migratory strategy, age, or weight. For both dependent variables, the ranking of models was identical (clutch size) or similar (nest fate) when including data beyond the first year after capture for each bird (Tables 6 and 7 vs. Appendix S1).

4 | DISCUSSION

We found that the willow ptarmigan population in the study area was partially migratory, and most (73%) of the individuals decided to carry out a seasonal migration from winter to summer areas rather than remaining resident. Similar migratory strategies have been reported from several other species of Galliformes, including spruce grouse *Falcipennis canadensis* (Herzog & Keppie, 1980) and blue grouse *Dendragapus obscurus* (Cade & Hoffman, 1993). Partly in line with our first prediction, we found that body weight related to the decision to migrate or to remain resident. This effect was only found among juvenile birds, where individuals with high body weight had a higher probability of remaining in the winter area. Among adult females, body weight did not appear to influence the decision to migrate or remain resident. In contrast with our second prediction, we found that migration decision was a fixed strategy once established, and individuals for which data on more than one seasonal migratory decision was available, showed a high degree of repeatability in migratory behavior. Finally, we found no support for our third prediction, as resident female willow ptarmigan had similar reproductive success to migrants.

TABLE 3 Distance moved from winter to summer area (first year of data after capture only) and weight of juvenile and adult female willow ptarmigans. N is the total number of movement distances observed. For adults, the numbers in parentheses include all observations, both from winter to consecutive summer and from summer to consecutive winter. Weight data are from capture during winter (March), rounded to nearest 5 g

	Age	Min.	Mean	Median	Max.	*N*
Distance (km)	Juv	0.0	7.8	4.5	30.0	33
	Ad	0.0	9.9 (9.6)	6.8 (7.0)	46.5 (46.5)	40 (71)
Weight (g)	Juv	520	590	590	670	33
	Ad	530	600	600	670	40

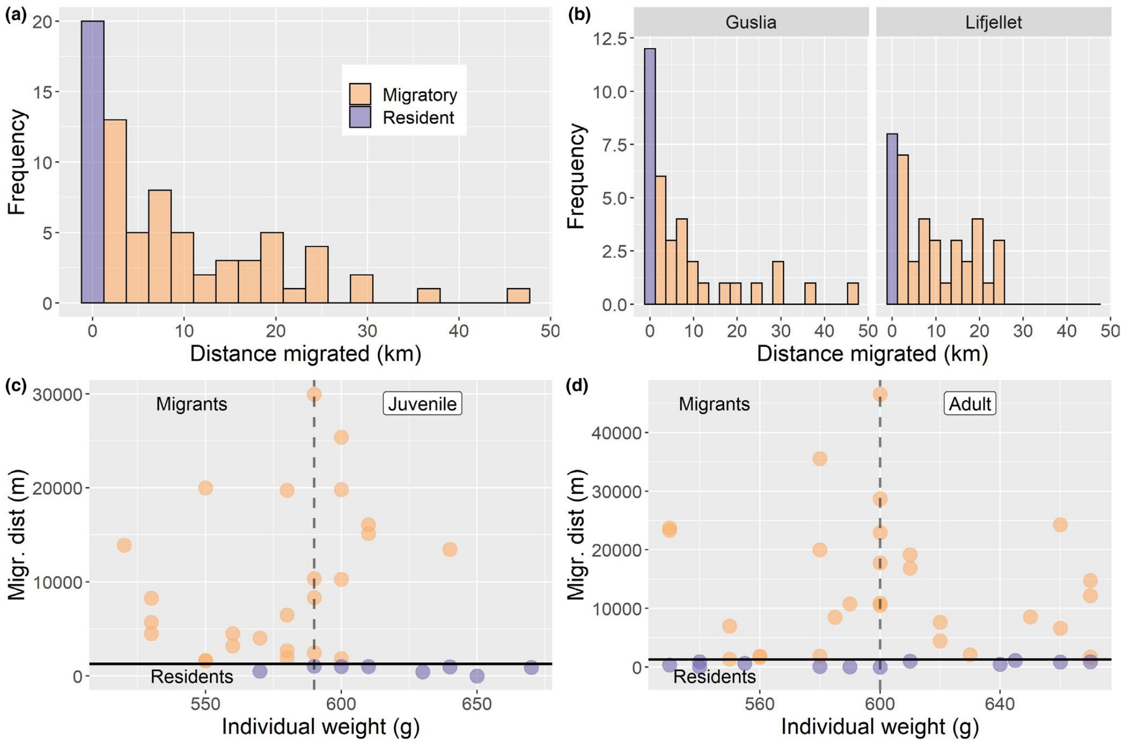

FIGURE 4 (a) Distribution of seasonal migration distances for female willow ptarmigan. Purple bar represents resident individuals, and orange bars represent migrants. See Figure 2 for definition of resident and migratory individuals. (b) Migration distance plotted for each capture site. (c) Distances migrated plotted against body weights of individual juvenile birds. Dashed vertical line represents mean and median weight and solid horizontal line marks the threshold movement distance separating residents and migrants (1276 m). (d) Same as c, but for adult birds. Purple dots represent migrants, whereas orange dots represent residents. In all panels, only winter-to-summer transitions are included, and only first year of data for each bird

TABLE 4 Candidate models and model statistics for modeling migration strategy (migrate vs. remain resident) as a function of age (juvenile or adult) and body weight for female willow ptarmigan. Results from generalized linear models (GLMs) with binary response (1 = migrated, 0 = remained resident) and logit link function, assuming binomial error distribution. Only winter-to-summer migratory decisions are included

Response	Model	K	AIC_c	ΔAIC_c	AIC_cWt	CumWt
Migratory strategy	Weight + Age + Weight × Age	4	82.84	0.00	0.80	0.80
	Weight	2	87.50	4.66	0.08	0.88
	Intercept	1	87.78	4.94	0.07	0.95
	Age	2	89.60	6.75	0.03	0.97
	Weight + Age	3	89.61	6.76	0.03	1.00

4.1 | Migration strategy in relation to age and body weight

One key finding of our study was that juvenile willow ptarmigan with small body sizes had a higher probability of migrating. The body size hypothesis posits that large body sizes will be advantageous to endure thermal variations and variation in food availability in harsh winter climates, and winter survival is generally high and stable in willow ptarmigan (Israelsen et al., 2020). Second, our data do not allow for an efficient test of this hypothesis because we only included birds with a shared winter area. Below, we discuss the likely importance of the dominance and the arrival time hypotheses for our results.

As posited by the dominance hypothesis, individuals with high body weight should have a competitive advantage to smaller individuals, forcing smaller individuals to migrate (Gauthreaux, 1982). For the dominance hypothesis to work, there must be an

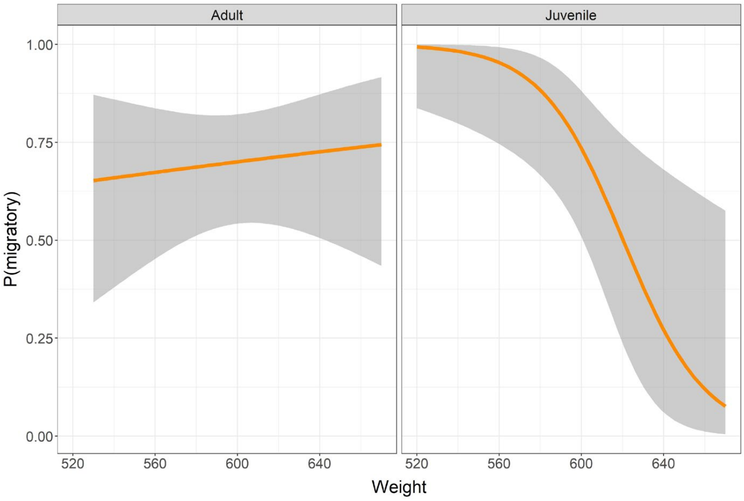

FIGURE 5 Estimated relationship (solid line) between body weight (g) and the probability of deciding to migrate in adult and juvenile female willow ptarmigan. The shaded ribbons represent 95% confidence interval. Only winter-to-summer transitions are included, and only first year of data for each bird

TABLE 5 Candidate models and model statistics for modeling movement distance as a function of age (juvenile or adult) and body weight for female willow ptarmigan. Results from linear models (LMs) with continuous response assuming Gaussian error distribution. Only winter-to-summer transitions are included, and only first year of data for each bird

Response	Model	*K*	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt	CumWt
Distance	Intercept	2	298.58	0.00	0.48	0.48
	Weight	3	300.60	2.02	0.17	0.65
	Age	3	300.70	2.12	0.16	0.81
	Weight + Age + Weight × Age	5	301.16	2.58	0.13	0.94
	Weight + Age	4	302.82	4.24	0.06	1.00

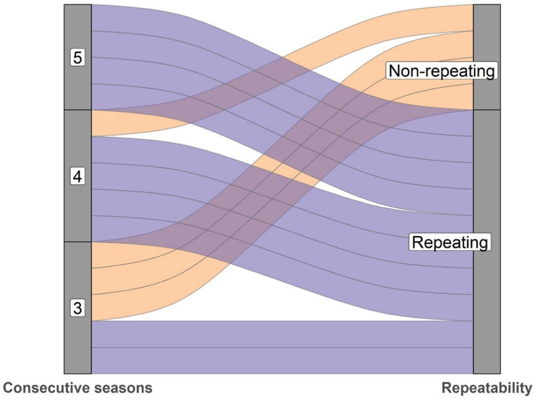

FIGURE 6 Repeatability of decision to migrate or remain resident between individuals. Purple bands = individuals with 100% repetition in migration decision between consecutive seasons. Orange bands = individuals that made different migration decisions in different seasons or years. Each band represents one individual

intraspecific competition for limited resources such as food or nest sites (Matthysen, 2005; Newton, 1998). Nesting sites close to the wintering grounds might be a limited resource (Gillis et al., 2008), and large dominant individuals might occupy the best breeding territories forcing juvenile ptarmigans to migrate to find a suitable breeding territory. This may be the case in the wintering areas where ptarmigan density is high during the winter months, and smaller (less dominant) individuals must migrate to find a suitable breeding territory in spring. Although two previous studies on dispersing juvenile willow ptarmigans in Scandinavia found no density dependence in dispersal rates (Brøseth et al., 2005; Hörnell-Willebrand et al., 2014), intraspecific competition driven by positive density-dependent factors might still be an important driver of partial migration in our study population.

Several studies have found support for the arrival time hypothesis as a driver of partial migration (Fudickar et al., 2013; Ketterson & Nolan, 1976; Lundblad & Conway, 2020), but lack of data on the when the females arrived in their breeding territories prevented us from testing this hypothesis explicitly. However, willow ptarmigans to some extent adjust the start of the breeding season to the timing of spring (Myrberget, 1986), hence, earlier spring leads to an early start to the breeding season. Resident ptarmigans may have an advantage in occupying high-quality territories prior to migrating individuals, and this might be particularly true in years with mild winters and early spring.

Our finding that the decision to migrate or remain resident depended on body weight in juveniles but not in adults is only partly in

TABLE 6 Candidate models and model statistics for modeling number of laid eggs as a function of migratory strategy (migration vs. resident in wintering area), age (juvenile or adult), and body weight for female willow ptarmigan. Results from generalized linear models (GLMs) with count response and log link function, assuming generalized Poisson error distribution (see methods)

Response	Model	K	AIC_c	ΔAIC_c	AIC_cWt	CumWt
N eggs	Intercept	2	209.42	0.00	0.32	0.32
	Age	3	209.91	0.49	0.24	0.56
	Weight	3	211.33	1.91	0.12	0.68
	Migratory strategy	3	211.65	2.23	0.10	0.78
	Age + Weight	4	212.17	2.74	0.08	0.86
	Age + Migratory strategy	4	212.21	2.78	0.08	0.94
	Migratory strategy + Weight	4	213.62	4.20	0.04	0.98
	Migratory strategy + Age + Weight	5	214.53	5.11	0.02	1.00

TABLE 7 Candidate models and model statistics for modeling nest fate as a function of migratory strategy (migration vs. remain resident in wintering area), age (juvenile or adult), and body weight for female willow ptarmigan. Results from generalized linear models (GLMs) with binary response (1 = hatched, 0 = abandoned/predated) and logit link function, assuming binomial error distribution. Only data from first year after capture are used

Response	Model	K	AIC_c	ΔAIC_c	AIC_cWt	CumWt
Nest fate	Intercept	1	79.64	0.00	0.40	0.40
	Migratory strategy	2	81.56	1.93	0.15	0.56
	Age	2	81.73	2.10	0.14	0.70
	Weight	2	81.77	2.14	0.14	0.83
	Age + Migratory strategy	3	83.72	4.09	0.05	0.89
	Weight + Migratory strategy	3	83.80	4.16	0.05	0.94
	Age + Weight	3	83.94	4.30	0.05	0.98
	Migratory strategy + Weight + Age	4	86.04	6.40	0.02	1.00

line with the dominance hypothesis. However, if migration in juveniles is affected by density-dependent factors, such as limitations in available territories, the dominance hypothesis may explain partial migration in juvenile ptarmigan.

4.2 | Repeatability of migration strategy

Once established, migratory behavior seems to be a relatively fixed trait in our study population, and the repeatability in migration decisions within individuals was very high. Our findings are in line with several studies on breeding partial migratory populations, which have found migratory strategy to be fixed within individuals (Chambon et al., 2019; Gillis et al., 2008). For example, in a breeding partial migratory population of American crow *Corvus brachyhynchos* in USA, Townsend et al. (2018) found that migratory strategy was fixed within individuals, the proportion of migrants was 78% and with high breeding site fidelity. Interestingly, bird populations that breed sympatrically but winter allopatrically seem to have a higher degree of non-fixed migration behavior (Dale et al., 2019; Hegemann et al., 2015; Lundblad & Conway, 2020).

A potential benefit of a fixed migratory strategy may be less exposure to unfamiliar habitat, and higher mortality rates that are associated by switching breeding sites between years (often referred to as breeding dispersal) have been reported (Bonte et al., 2011; Daniels & Walters, 2000; Greenwood & Harvey, 1982). Returning to the same breeding territory may also be beneficial due to familiarity with food resources and shelter from predators, which in turn leads to a more efficient use of resources (Greenwood & Harvey, 1982). This effect may be enhanced in individuals that remain resident all year, and according to Buchan et al. (2019) most studies on the consequences of partial migration reported higher mortality in migrants than in resident individuals. The high repeatability in migratory strategy within willow ptarmigans may be caused by resistance against moving to unfamiliar breeding wintering sites.

4.3 | Reproductive success in relation to migration strategy

In contrast to our third prediction, we did not find any statistical support for higher reproductive success (measured as clutch size and nest fate) of resident birds. Our prediction was based on the "best of a bad job" hypothesis (Lundberg, 1987), positing that migration is a losing strategy that should lead to reduced fitness. Based on a multi-taxa assessment, Buchan et al., 2019 reported that although most studies reported fitness differences between resident and migrants (73% of the studied populations reported higher fitness of residents, 22% reported higher fitness of migrants, and 5% reported equal fitness), fitness differences were most often caused by differences in survival. They argue that the reason for this finding can be that anthropogenic changes reduce the survival of migratory individuals. Our finding that migratory decisions seem to be relatively fixed once established appears to be in line with the finding that fitness does not differ between the strategies in our study population. However, there may be differences in survival between residents and migrants, and we suggest further investigations to be carried out to get a better understanding of the consequences of partial migration in the willow ptarmigan.

For fitness to be equal between the two migratory strategies, theoretical studies suggest that higher survival in migrants must offset the increased nesting success in residents (Chapman et al., 2011; Lundberg, 1987). Reduced risk of predation (Hebblewhite & Merrill, 2007; Skov et al., 2011), escape from harsh climatic conditions, and better forage are pointed at as important factors enhancing survival in migrants. Our results showed that a large proportion of the willow ptarmigan population carried out seasonal migrations, with little variation between years. If migratory strategy is genetically determined, the fitness trade-off between migrating vs. resident strategies may be frequency dependent where the fitness payoff for each genotype increases or decreases with the genotype's frequency in the population (Heino et al., 1998; Lundberg, 1987). Negative frequency-dependent selection rewards the strategy with lowest frequency in the population, i.e., selection is density dependent. The population may reach an equilibrium in an evolutionary stable state between migrants and residents where both strategies (genetic morphs) yield the same fitness. The frequencies of migrants and residents may stabilize at any ratio, and the small between-year changes in the migrants:residents ratio in this willow ptarmigan population may indicate that it is in equilibrium. This may explain why we did not find any differences in reproductive success between the two strategies. If this is indeed the case, migrants are not making "the best of a bad job" where migration is the losing strategy in terms of both survival and reproductive success, and contradicts the findings of most empirical studies (Buchan et al., 2019; Chapman et al., 2011).

To conclude, we found that willow ptarmigans in central Norway were partially migratory, making them well suited for studies of the evolution of partial migration. The probability of remaining resident in the wintering area increased with increased body weight in juveniles, but not in adults. We found partial support for the dominance hypothesis for explaining partial migration, but cannot exclude the arrival time hypothesis as a potential driver of the observed pattern. The migratory decisions displayed at the juvenile stage appeared to become fixed throughout the individuals' lifetime. We found no difference in average reproductive success between migratory strategies, which indicates that both strategies yield equal fitness unless there are differences in survival between the strategies.

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AUTHOR CONTRIBUTION

Øyvind Arnekleiv: Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Katrine Eldegard:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review & editing (equal). **Pål F. Moa:** Conceptualization (supporting); Data curation (supporting); Funding acquisition (supporting); Project administration (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review & editing (supporting). **Lasse F. Eriksen:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review & editing (equal). **Erlend B. Birkeland Nilsen:** Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Validation (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review & editing (lead).

DATA AVAILABILITY STATEMENT

Data and R-code (Arnekleiv et al., 2022) are available from a time-stamped registered archive at Open Science Framework (DOI: https://doi.org/10.17605/OSF.IO/CY68W).

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PAPER IV

Climatic variation affects seasonal survival of an alpine bird species

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